STUDIES OF THE ROOT REGENERATION POTENTIAL OF *Pinus radiata* D. DON SEEDLINGS

by

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STATEMENT OF ORIGINALITY

Except where specific acknowledgement is given the research work reported in this thesis is entirely that of the author.

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ABSTRACT

The ability of bare-rooted seedlings to survive and achieve maximum early growth once outplanted to the forest can influence the success of plantation establishment. This ability depends largely on the quality of seedlings produced, particularly their physiological condition. A critical indicator of physiological condition of seedlings is their potential for root regeneration (RRP). Numerous factors in the nursery and in the field influence RRP. This study investigates the effect of some environmental factors and nursery cultural practices on the RRP and shoot growth of *P. radiata* seedlings. Environmental factors studied included nutrients, light intensity, photoperiod, air and soil temperature. The cultural practices examined were root- and shoot-pruning. All experiments were conducted in controlled environments. RRP of seedlings was assessed by counting numbers and measuring lengths of new root produced in a set period of time.

Given an adequate supply of nutrients throughout the growing period *P. radiata* seedlings showed a high capacity to regenerate roots following root-pruning and replanting into conditions of limited nutrient supply (-N, -P, -NP), whereas seedlings grown in a nutrient deficient situation showed poor growth and RRP when root-pruned and replanted into favourable conditions.

Photoperiod had little effect on RRP of seedlings, although shoot growth and root extension were slightly better under longer days. Growth and RRP of seedlings were depressed by low light intensity.

Seedlings showed a remarkable capacity to regenerate roots over a wide range of air ($8^{o}/4^{o}C$ - $30^{o}/25^{o}C$) and soil (5^{o}-$35^{o}C$) temperatures. Where air and soil temperatures were not independently controlled maximum shoot growth and RRP occurred within the temperature range of $21^{o}/16^{o}C$ to $27^{o}/22^{o}C$. Where air and soil temperatures were independently controlled RRP was high at soil temperatures of $20^{o}C$ to $30^{o}C$, with a corresponding soil heat sum of 480 to 720 degree-hours. Net photosynthesis, translocation of photosynthates to the roots and seedling water content were also high within this range.

Under a favourable day temperature ($27^{o}C$) with a small day/night differential seedlings produced longer roots, but where the day/night differential was greater seedlings directed more growth energy into height increase.

The greater the proportion of shoot or root pruned from seedlings the lower the RRP. However, given favourable environmental conditions, even the most severely root-pruned seedlings showed evidence of root initiation.

Root-pruning *per se* caused a disturbance in a number of physiological processes including photosynthesis, dark respiration, stomatal behaviour and moisture relations. Under favourable environmental conditions seedlings were able to adjust to this disturbance within eight days of being root-pruned. There followed a gradual resumption of both shoot and root growth.

The practical implications of these findings in relation to nursery practice and seedling establishment are discussed. In conclusion, the quite spectacular success of *P. radiata* as a plantation species is seen as being due, at least in part, to the extraordinary capacity of this species to regenerate roots under a wide range of environmental conditions.

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CHAPTER 1

INTRODUCTION

1.1 GENERAL

Increasing demands for forest products have sparked much interest in plantation forestry throughout the world. In Australia, a softwood planting program began in the late 1800's and has continued in attempts to overcome the shortfall in timber supplies from the hardwood forests (Florence and Shepherd, 1975), and to provide a continuous source of wood for domestic industry. The fast growth rate and high productivity of the exotic softwoods have enabled Australia to produce a significant quantity of wood for present needs but predictions of an increased wood demand early in the twenty-first century suggest the productivity of Australia's forests need to be increased by approximately 100 per cent to meet the stated objective of net self-sufficiency (Forwood, 1974). The establishment of additional plantations of fast growing species appears to be a satisfactory solution to this problem. A target of 1.14 million hectares of plantation (softwood and hardwood) has been proposed (Forwood, 1974).

Pinus radiata D. Don is the most important commercial exotic softwood planted in the Southern Hemisphere. In 1975 some 35,250 hectares of *P. radiata* plantations were established in Australia (approximately 66% of the total area planted), bringing the total area of *P. radiata* plantations to 394,400 hectares (For. Timb. Bur., 1976). In New Zealand, 19,500 hectares of *P. radiata* were established in 1975 giving a total of 240,600 hectares planted to *P. radiata* (Rept. Dir. Gen. For., N.Z., 1976).

Plantations may be established on a wide variety of sites ranging from high quality sites for seedling growth to those which are marginal for growth (Brown and Hall, 1968; Florence, 1969; Hopkins, 1971b; Shepherd, 1971). In all instances cultural practices of initial site preparation, and applications of fertilizers and weedicides can markedly influence the initial survival of seedlings and their subsequent growth (Windsor, 1972; South, 1975; Woods, 1976; Menzies, 1977).

The influence of site and cultural treatments on seedling growth has also been demonstrated quite dramatically by reported losses in productivity of *P. radiata* stands in the second rotation on sites in South Australia and New Zealand (Stevens and Bond, 1957; Lewis and Harding, 1963; Stone and Will, 1965a; Keeves, 1966; Bednall, 1968; Whyte *et al.*, 1969; Berg, 1975).

The decline in productivity in the second rotation has been attributed to a variety of factors including depletion of nutrient supply, depletion of soil water, inhibition of root or seedling growth due to the presence of toxic residues or soil micro-organisms, changes to the establishment practices due to residual stumps and roots and changes in the genetic constitution of the planting stock (Lewis and Harding, 1963; Stone and Will, 1965a; Raupauch, 1967; Bednall, 1968; Florence and Lamb, 1971; For. Timb. Bur., 1971a; Squire, 1975).

Recent studies of re-establishment of *P. radiata* on the second rotation sites have indicated that site cultivation and applications of fertilizers and weedicides can improve survival and maximum early growth to the estimated site potential (Wds. For. Dept., S.A., 1970, 1975, 1976a,b; W.A. For. Dept., 1974, 1975, 1976; Boardman, 1974; Berg, 1975; Woods, 1976). Additionally, the nutrient status of the seedlings at planting appears to influence their subsequent performance (Donald, 1968; Woods, 1976).

In addition to cultural treatments within the plantation itself and the climatic factors which prevail during and following planting, the condition of the seedlings at the time of planting can play a major role in determining the rate at which seedlings are able to establish themselves, the rate of development of the plantation, and its ultimate productivity.

Factors such as nutrient resources available within the seedlings, potential for root regeneration and tolerance to drought may all influence the rate and success of plantation establishment.

1.2 SEEDLING CONDITION AFFECTING SURVIVAL AND ESTABLISHMENT

Irrespective of planting conditions part of the seedling response following outplanting is determined by the genetic, morphological and physiological condition of the seedling at the time of planting. Numerous authors stress that the physiological qualities of the seedling are more important than either morphological

characteristics or even most site conditions (Wakeley, 1948, 1954; Stone, 1955, 1967a; Stone and Schubert, 1959a,b; Smith and Allen, 1962; Stone and Benseler, 1962; Stone *et al.*, 1962, 1963; Walters and Kozak, 1965; Nelson and Switzer, 1966; Hermann and Lavender, 1967; Schubert and Adams, 1971; Stone and Jenkinson, 1971; Armson and Sadreika, 1974; van den Driessche, 1976). The seedling condition at the time of planting is in turn determined by conditions in the nursery in which the seedlings are raised. The root regenerating potential (RRP) has been found to be a good index of the physiological condition of planting stock (Stone and Jenkinson, 1971). This is controlled by cultural treatments, and the climatic and edaphic environment of the nursery and planting site (Bilan, 1961; Stone *et al.*, 1963; Schubert and Baron, 1965; Krugman and Stone, 1966; Stone, 1966, 1967a,b; Larson, 1970; Larson and Whitmore, 1970; Stone and Jenkinson, 1970, 1971; Day and Stupendick, 1974; Day, Stupendick and Butler, 1976; Abod, 1977).

1.2.1 Inherent Factors

Inherent factors largely control the growth and development of seedlings (Kozlowski, 1955; Leopold and Kriedemann, 1975). Growth patterns vary among species of the temperate and tropical regions of the world (Kozlowski, 1955; 1971a; Kramer and Kozlowski, 1960; Zahner, 1968). With most temperate species a periodicity of growth and development is observed in both shoots and roots. For example, shoot and root development are characterized by pronounced seasonal patterns of growth and dormancy. Reactivation of root growth and shoot flushing in spring, and setting of dormant buds and cessation of root growth in autumn parallel the seasonal changes in the environment (Laing, 1932; Kozlowski, 1955, 1971a; Lyr and Hoffmann, 1967; Merritt, 1968; Zahner, 1968; Sutton, 1969; Lathrop and Mecklenburg, 1971; Wareing, 1971).

Inherent seasonal patterns in the ability of seedlings to regenerate roots has been reported for a number of nursery-grown conifers including *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus ponderosa* Laws. (Stone, 1955, 1966, 1967a,b; Schubert and Stone, 1958, 1959a,b; Stone *et al.*, 1962, 1963; Winjum, 1963; Todd, 1964; Schubert and Baron, 1965; Krugman and Stone, 1966; Hermann and Lavender, 1967; Stone and Jenkinson, 1971), *Pinus taeda* L. (Bilan, 1961), *Taxus hunnewelliana* Rehd. (Lathrop and Mecklenburg, 1971), *Picea glauca*

(Moench) Voss, *Picea mariana* (Mill.) B.S.P. and *Pinus banksiana* Lamb. (Stupendick, 1973; Day and Stupendick, 1974; Day, Stupendick and Butler, 1976). All of these species set dormant buds and exhibit distinctive inherent growth patterns which can be largely modified by environmental factors. The possible modifications which can be in terms of either quantity and/or timing of growth, again vary with species.

The existence of periodic growth patterns in temperate species restricts the time at which seedlings may be lifted and planted out. Lifting and planting must be carried out at the time when seedlings are physiologically ready, that is, when RRP is high. This is particularly important when the planting site requires rapid root regeneration (Stone, 1967a, Stone and Jenkinson, 1971).

Unlike the temperate species *P. radiata* and most tropical and sub-tropical pines do not exhibit a definite dormant period. The pattern of shoot growth of *P. radiata* is variable in that it continues indefinitely or recommences whenever environmental conditions are favourable (Fielding, 1955, 1966; Shepherd, 1964; Cremer, 1972). Krugman, Stone and Bega (1965) found that RRP of this species, like its shoot growth, may continue at a high rate throughout the year with only periodic increases in root growth coinciding with flushing at the onset of more favourable environmental conditions. Thus, *P. radiata* seedlings are intrinsically capable of being raised, lifted and planted at any time of the year (Moberly, 1970). However, this characteristic may be disadvantageous for coping with harsh field conditions including frost and drought, unless the seedlings are adequately conditioned in the nursery.

1.2.2 Nutritional Status

The nutritional status of seedlings at the time of lifting is largely determined by the availability of nutrients in the nursery soil (Switzer and Nelson, 1963; Meyer and Tukey, 1965, 1967; Benzian and Freeman, 1967; Meyer and Spiltstoesser, 1971; Sanada, 1971; Will, 1971a; Knight, 1973; Benson, 1976a; van den Driessche, 1977), and the ability of seedlings to absorb them. Nursery soil management is, therefore, an important nursery practice influencing seedling nutritional status as well as other morphological and physiological characteristics of seedlings (Armson and Sadreika, 1974). Once out-planted, the seedlings must rely on their accumulated nutrient reserves

until new roots are extended into the soil to reach and absorb nutrients. In this sense, nutrient reserves appear to be an important factor influencing seedling survival and establishment.

Numerous studies with many species, all indicate that improved nursery fertilization throughout the growth period and/or prior to lifting produces seedlings with large nutrient reserves and increased survival and growth rates once outplanted (Wilde *et al.*, 1940; Allen and Maki, 1955; Stoeckeler and Jones, 1957; Switzer and Nelson, 1963; Anderson and Gessel, 1966; Smith *et al.*, 1966; Benzian and Freeman, 1967; Burns and Brendemeuhl, 1971; Sanada, 1971; Machek, 1972/1973; Benzian *et al.*, 1974; Lüpke and Lewinski, 1974; Ostrowska, 1974; Mullin and Bowdery, 1977). Donald (1968) found that *P. radiata* seedlings raised with inorganic fertilizer in the nursery grew significantly better in diameter and height during the first year in the field than those raised without fertilizer. Woods (1976) also describes a field trial with *P. radiata* seedlings showing that seedling height growth after outplanting was improved by addition of nitrogen fertilizer in the nursery. However, in some studies it has been shown that fertilization prior to lifting has a detrimental effect on field survival (Ursic, 1956; Shoulders, 1959a). Shoulders (1959a) concluded that fertilizer application prior to lifting may be useful when nutritional levels are low, but that wholesale application may be damaging to seedlings.

Seedling response to fertilizer may be evaluated in a number of ways. One of the most beneficial aspects of improved nursery fertilization is an increase in the number of seedlings of plantable size (Stoeckeler and Jones, 1957; Stoeckeler and Arneman, 1960; Benson, 1976a; Minko and Craig, 1976). Also, the field performance of *P. radiata* seedlings during the early years after transplanting largely depends on seedling size (Fowells, 1953; Anstey, 1971; Pawsey, 1972; Minko, 1972, 1974; Benson, 1976a; Benson and Shepherd, 1976; Minko and Craig, 1976). On the other hand, fertilization may reduce seedling quality by promoting more shoot growth than root growth (Brouwer, 1962; Benson, 1976a), resulting in seedlings with a low root:shoot ratio which are poorly adapted physiologically to survive under adverse conditions of drought or frost (Shirley and Meuli, 1939; Wilde and Voigt, 1949; Shoulders, 1959a; Stoeckeler and Arneman, 1960; Benson, 1976a). Timing fertilizer applications late in the season has been shown to increase drought resistance in a number of conifers

(Kopitke, 1941; Anderson and Gessel, 1966) but fertilization of *P. radiata* which has no real dormant period can induce succulent new growth which may be susceptible to frost and drought damage.

1.2.3 Moisture Status

Moisture status is a critical factor influencing survival and early growth of seedlings once outplanted to the forest (see authors cited by Wakeley, 1954; Williams, 1975; Lavender and Hermann, 1976). Factors such as water loss from seedlings during lifting, grading, packing, storage and transit to the planting site can determine the moisture status of seedlings at planting (Tarrant, 1964; Schubert and Adams, 1971; Armson and Sadreika, 1974; Benson, 1976b). The balance between transpiration and absorption of moisture determines whether or not critical internal water stresses develop in plants (Newton, 1973; Kozlowski and Davies, 1975). If the root surface is inadequate to supply the water lost by the shoots through transpiration, internal water deficits will inevitably follow. The size and growth activity of the shoot at the time of planting can affect the balance between transpiration and absorption and hence initial survival of the seedling. Shoots which are large relative to root surface during the root regeneration period are not desirable when evaporative stress is high because this results in moisture stress in seedlings (Stone, 1966). Where shoots are growing actively, transplanting frequently results in wilting or subsequent death of the leader due to the development of adverse internal water balances (Rook, 1969a; Benson, 1974). Shoot-pruning (Stoeckeler and Jones, 1957; Anon., 1968; Bacon, 1975; Lavender and Hermann, 1976) and needle clipping (Wakeley, 1954; Langdon, 1955) have been used for some species in attempts to improve the root:shoot balance of seedlings under the assumption that higher root:shoot ratios will reduce transpiration and the probability of critical water stress developing in seedlings.

Lifting and transporting of seedlings can cause gross mechanical damage to seedling root systems. Many of the root tips and long absorbing roots are broken or desiccated before seedlings are planted (Wakeley, 1954 and others cited by Sutton, 1969). Consequently, an immediate and severe water deficit could develop in the transplanted seedling (Kozlowski, 1968; Kozlowski and Davies, 1975). For *P. radiata*, severe water deficits due to transplanting have resulted

in wilting and eventual death of the whole seedling (Rook, 1969b; Benson, 1974, 1976a; Benson and Shepherd, 1977). Recent investigations with *Picea abies* (L.) Karst by Gürth (1970), Lüpke (1973) and Havranek (1975), as discussed by Lavender and Hermann (1976), also showed that damage to the root systems of seedlings transported from the seedbed to the planting site reduced water uptake and was a principal reason for the observed transplant shock.

Despite the damage to roots caused by lifting, transporting, and planting, seedlings may be able to take up water for a short time after planting given adequate moisture in the soil (Kramer, 1933, 1946; Kramer and Bullock, 1966; Chung and Kramer, 1975). However, for survival it is essential that seedlings regenerate new roots to explore new soil areas to tap water and nutrient reserves. High physiological quality of seedlings, in terms of root regeneration potential (RRP), therefore improves survival principally by ensuring that water uptake in seedlings immediately after planting equals or exceeds water loss (Wakeley, 1948, 1954; Kozlowski and Davies, 1975; Lavender and Hermann, 1976). Havranek (1975) observed that *P. abies* seedlings with low RRP suffered severe water loss and growth check which adversely affected formation of primordia for the next years terminal growth. Day and MacGillivray (1975) similarly found that *Picea glauca* seedlings with lowest RRP were under the highest moisture stress when measured 40 days after transplanting into various soil moisture regimes.

Because of the greater susceptibility of *P. radiata* seedlings to environmental stresses (i.e., drought, frost) due to their active growth habit, efforts are made to condition seedlings to withstand the stresses to which they are subject during and after planting to the forest. Increased resistance to drought, in particular, can be increased in *P. radiata* seedlings by undercutting the roots and root wrenching (Rook, 1969a, 1971; Cameron *et al.* 1970; van Dorsser and Rook, 1972; Benson, 1974; Benson and Shepherd, 1977) or by restricted watering (Rook, 1973).

Undercutting the roots and root wrenching modify many morphological and physiological aspects of seedling growth. After outplanting, wrenched seedlings produce a large number of active root tips with a greater total surface area. Such root systems are more efficient in absorbing water and are able to maintain high internal water contents under adverse conditions (Cameron and Rook, 1969b;

Rook, 1969b, 1971; van Dorsser and Rook, 1972; Benson, 1974; Benson and Shepherd, 1977). The more favourable water status enables the seedlings to photosynthesize and grow soon after planting while unwrenched seedlings succumb more readily to unfavourable conditions.

Modifications in watering in the nursery can also influence the development of drought resistance in seedlings. Early experiments by Shirley and Meuli (1939) showed that drought resistance of *Pinus resinosa* Ait., *Pinus strobus* L. and *Pinus banksiana* was increased by subjecting seedlings to moderate soil drought during the period of vegetative activity in the nursery. Similarly, Rook (1973) improved the water status of *P. radiata* seedlings by restricted watering six weeks prior to transplanting. These seedlings had a more efficient stomatal regulation of water loss and enhanced RRP after planting. Non-stressed plants produced fewer roots; a condition critical to survival on some sites. Unterschuetz *et al.* (1974) also found that restricted irrigation of *Pseudotsuga menziesii* seedlings resulted in a lower decrease in transpiration in response to low plant water potential than did well-watered plants.

While conditioning seedlings prior to lifting is widely practised to increase field performance of *P. radiata* under a wide range of environmental conditions the importance of maintaining favourable moisture supply throughout the growing season in the nursery cannot be ignored. Minko (1976) found that *P. radiata* seedlings grown under soil moisture potentials of -0.3 and -0.8 bars performed better once outplanted than those grown under soil moisture potentials of -1.5 and -1.9 bars. In the former conditions, the seedlings produced were of higher quality, i.e., greater root development, shoot height and diameter, which accounts for the greater success in the forest.

1.2.4 Stored Food Reserves

Seedlings lifted from the nursery usually undergo severe physiological shock, and it takes some time before roots establish intimate contact with the soil. Because of their restricted ability to take up water and nutrients, initial seedling survival and establishment must also depend on the food reserves accumulated in the nursery.

Wakeley (1954) suggests that stored food reserves may be required for the development of new root tissue to allow water uptake.

Evidence for a relationship between food reserves and root growth has been reported by a number of researchers. Hartmann and Kester (1968) and Kozlowski (1971a) review the importance of carbohydrates in the rooting of plant cuttings, and Richardson (1953b, 1956) showed that when photosynthesis is reduced in *Acer saccharinum* L. seedlings by lowering the light intensity or the temperature, root growth depended on food reserves in the leaves. Such a decline in photosynthesis could be expected in seedlings after planting (e.g. Abod, 1977). More recently Little (1970) concluded that high levels of starch in the shoots of *Abies balsamea* (L.) Mill. may improve their root growth following spring transplanting. In another study, Etter and Carlson (1973) suggested that the supply of sugar from the shoot may be a deciding factor in the occurrence of root growth in stored *Pinus contorta* Dougl. after tranplanting. In contrast, Gilmore (1962, 1964) found no correlation between root growth of *Pinus taeda* and carbohydrate content of the root at the time of planting. Ronco (1973) similarly found that survival of field planted *Picea engelmannii* Parry was not correlated with food reserves in seedlings above the critical level but, up to this critical level carbohydrate reserves were important to survival.

Fluctuations in food reserves, related to the seasonal shoot and root growth pattern in transplanted seedlings, have been reported. Krueger and Trappe (1967) observed a nearly coincident timing during winter and spring of carbohydrate peaks and maximum RRP in *Ps. menziesii*. They inferred from this an important role of food reserves in RRP. Winjum (1963) also working with *Ps. menziesii* found that non-reducing sugar contents in the shoot paralleled root production throughout the year.

The food reserves of seedlings can be modified prior to planting by various nursery practices. Undercutting of roots and root wrenching cause significant changes in sugar and starch concentrations of seedlings (Rook, 1971; Bacon, pers.comm.). Rook (1971), for example, showed root wrenching *P. radiata* seedlings at weekly or two-weekly intervals increased starch levels slightly over unwrenched seedlings. Wrenching at monthly intervals, however, greatly increased the levels of reducing and total soluble sugars and starch compared to seedlings wrenched at weekly or two-weekly intervals.

Ronco (1973) found that extended cold storage after lifting severely depleted food reserves. Ronco considers that reductions in

available reserves may not in themselves greatly affect the survival of planted seedlings, but adverse conditions of the site may reduce reserves below a critical level.

An additional role of food reserves in relation to field survival could be related to frost hardiness. Wakeley (1948) and Levitt (1972) cite a number of authors who have examined this role of food reserves.

1.3 PURPOSE OF STUDY

In the light of the increasing importance of *P. radiata* as an economic species in many countries (e.g. Australia, New Zealand, South Africa, Chile), it is highly desirable that further detailed studies of the physiology of *P. radiata* seedlings with respect to plantation establishment be initiated. Seedlings must have the ability to regenerate new roots rapidly once outplanted to take full advantage of all the site has to offer during the first years of establishment. The factors influencing this initial root growth response following outplanting require serious attention. Studies on the survival, RRP and maximum early growth of *P. radiata* seedlings are limited.

The present study investigates the effects of various environmental factors and nursery practices on the physiological condition of *P. radiata* seedlings, with particular reference to root regeneration potential. Knowledge of these effects may help determine the critical factors influencing planting stock survival and maximum early growth after seedlings are planted out.

CHAPTER 2

ROOT REGENERATION POTENTIAL AND ENVIRONMENTAL FACTORS AFFECTING ROOT REGENERATION POTENTIAL

2.1 ROOT REGENERATION POTENTIAL

The physiological condition of the seedling, particularly its potential to regenerate roots (RRP) has received considerable attention since the early studies, with *Pinus ponderosa* and *Pseudotsuga menziesii*, pioneered by Stone and his co-workers in the 1950's (reviewed by Stone, 1966, 1967a,b; Stone and Jenkinson, 1971). The importance of RRP in terms of survival and establishment is well recognized (Schubert and Adams, 1971; Stone and Jenkinson, 1971; Armson and Sadreika, 1974; van den Driessche, 1976; Lavender and Hermann, 1976). In the assessment of RRP using Stone's technique (for details see Chapter 3, Section 3.3.4), seedlings are root-pruned and trimmed of remaining white root tips. The physiological effects that this treatment has on seedlings may be regarded as similar to those experienced by seedlings after root-pruning, undercutting and/or wrenching in the nursery or by seedlings lifted and planted to the forest. Because of this similarity, the response of seedlings under various treatment conditions would reflect the seedling's RRP not only once outplanted but also following such nursery practices.

Genetic (Chapter 1, Section 1.2.1) and the environmental factors of both the nursery in which seedlings are raised and of the planting site influence the ability of a seedling to regenerate roots. Of the environmental factors; soil moisture, light, and air and soil temperature have been given greatest attention in the study of RRP.

2.2 ENVIRONMENTAL FACTORS

2.2.1 Soil Moisture

There has been a series of studies reported by Stone and co-workers (Stone, 1966, 1967a, 1968, 1970) to determine the effect of soil moisture, varying from field capacity to just above the wilting point, on the RRP of 1-0 *Pinus ponderosa* seedlings. The authors found that the RRP of seedlings of this species was depressed by limiting soil moisture availability. The magnitude of depression was determined by the condition of the seedling at transplanting. Where

seedlings were transplanted when root growth was just commencing and the potential very high the roots continued to elongate in soils almost depleted of available moisture. Where root growth had not yet commenced or was potentially very low root elongation was restricted in low soil moisture. Larson and Whitmore (1970) in their study with 1+0 *Quercus rubra* L. seedlings transplanted into vermiculite and water with polyethylene glycol solutions of various osmotic potential found that shoot growth and the numbers, lengths, development of laterals and dry weight of regenerated roots decreased with a decrease in osmotic potential. Similar reductions in RRP have been reported by Day and MacGillivray (1975) for autumn-lifted 2+0 *Picea glauca* seedlings transplanted under limiting soil moisture conditions. At lower soil moisture contents root regeneration was delayed and the rate of root elongation much reduced. In a field study conducted on *Pinus taeda*, Bilan (1961) found that RRP was influenced by a number of environmental factors including soil moisture. It was found that the rate of growth of the lateral and main root was higher under favourable soil moisture conditions than during soil moisture stress.

The studies reviewed so far only deal with the effect of soil moisture in the planting conditions. In addition, soil drought in the nursery prior to lifting can also influence the capacity of seedlings to regenerate roots. This has been reported with *P. glauca* by Day, Stupendick and Butler (1976).

2.2.2 Light

Very little work has been reported on the influence of light on RRP. However, it is well recognized that light has a strong influence on root growth. Barney (1951), for example, found that there was a rapid rise in the rate of root growth of *P. taeda* seedlings with increased light intensity at low light intensities. Similarly, Stone (1967a) reported that root elongation in *Pinus ponderosa* was enhanced at a light energy of 42,000 ft-candle-hrs than at 35,500 ft-candle-hrs. In a more recent study with *Pinus caribaea* Mor. and *Pinus kesiya*, Royle ex Gordon, Abod (1977) found that RRP, dry matter production and shoot growth increased with increasing irradiance from 25 to 75 watts-m^{-2}. In another experiment Abod (1977) reported that RRP and photosynthesis of *P. caribaea* was reduced under 16% shade. Richardson (1953a) with *Acer saccharinum* L. and Webb (1976) with *Acer saccharum*

Marsh. seedlings found that any change in light intensity that affected photosynthesis resulted in concomitant changes in root elongation rates.

2.2.3 Temperature

Both air and soil temperature have a significant influence on the RRP of a seedling. Among the many early studies carried out on *P. ponderosa* in the United States (Stone and Schubert 1958, 1959a; Stone and Benseler, 1962; Stone *et al.*, 1963; Schubert and Baron, 1965; Krugman and Stone, 1966; Stone, 1967) most attention was focused on the effect of date of lifting and preconditioning temperature in the nursery on RRP. In relation to preconditioning temperature it was found that RRP varied with the number of hours seedlings were exposed to low night temperature following a regular growing season. High RRP was obtained for seedlings exposed to a greater number of hours of low night temperature (Schubert and Baron, 1965; Krugman and Stone, 1966; Stone, 1967a,b; Stone and Jenkinson, 1971).

In a study on the effect of site factors on the establishment of *P. taeda* Bilan (1961) also found that seasonal variation in air temperature greatly influenced the rate of root growth of transplanted seedlings. In winter when air temperature was low, RRP of seedlings was reduced. Abod (1977) found that with *P. caribaea* and *P. kesiya* maximum RRP was attained at moderate day temperatures (24^{o}-27^{o}C) and cool night temperatures (16^{o}-19^{o}C).

Apart from air temperature, soil temperature of the planting site also has a significant role in influencing the RRP of a seedling. It has been reported for a number of species including *P. ponderosa* (Schubert and Baron, 1958, 1959a), *Q. rubra* (Larson, 1970), *P. caribaea* and *P. kesiya* (Abod, 1977) that low soil temperatures in the order of 10^{o}-15^{o}C severely retard RRP of seedlings. For these species RRP appeared to be maximum between 20^{o}-30^{o}C. There are many other studies that can be cited in the literature dealing with root growth of a number of species under various air and soil temperatures (e.g. Barney, 1951; Lyford and Wilson, 1966; Larson, 1967; Lavender and Overton, 1972). However, no specific assessments of RRP were made in these studies.

It is apparent from the preceding review that RRP of seedlings is affected by various environmental factors. Thus in the study

reported here, a number of these factors including nutrients, light, air and soil temperature were examined.

CHAPTER 3

AN OUTLINE OF GENERAL EXPERIMENTATION

The facilities and apparatus used are outlined in this chapter together with a general description of experimental materials and methods. Specific experimental techniques are dealt with in the relevant sections.

3.1 CHOICE OF ENVIRONMENTAL FACTORS

Various environmental factors influence the growth and development of nursery seedlings. The effects of some of these factors on the root-regeneration potential of *P. radiata* seedlings has been investigated. Within the limitations of space and time, the following environmental factors were examined: air and soil temperatures, photoperiod, light intensity and soil nutritional status. The effects of shoot- and root-pruning, both standard nursery practices in *P. radiata* production were also examined.

3.2 FACILITIES AND APPARATUS

3.2.1 Phytotron Facilities - Glasshouses and Cabinets

Experiments were carried out at the C.S.I.R.O. CERES phytotron, Canberra and the Forestry Department, A.N.U. CERES, as described by Morse and Evans (1962), provides controlled environment space in both glasshouses and cabinets. Open glasshouses were maintained at the day temperature for eight hours (0830-1630) and at a night temperature 5°C lower for the remaining sixteen hours. Mean air temperatures were controlled within ± 1.5°C of the stipulated temperature. Relative humidity was kept above 40%. The northerly orientation of the glasshouses allows for maximum use of natural light. Eight hours of low incandescent lighting (0600-0800, 1600-2000) provides extended illumination of about 25 f.c. at plant height.

Naturally-lit 'C' and 'B' cabinets (Morse and Evans, 1962) within the glasshouses provide mean air temperature control within

± 0.25°C. Photoperiod can be precisely controlled, that is, extended by incandescent lamps or limited by automatic shutters. Higher relative humidity can be maintained in these cabinets compared to the glasshouse but day light intensity is reduced.

Artificially-lit LB cabinets (Morse and Evans, 1962) provide mean air temperature control to ± 0.25°C of the desired temperature and relative humidities above 40%. Fluorescent tubes (140 watts) supplemented by incandescent lamps provide constant radiation of 635-835μEm $^{-2}$sec^{-1} (3000-4000 f.c.) throughout the entire photoperiod.

The glasshouse at the Forestry Department is equipped with a thermostatically controlled heater and cooler. Glasshouse temperatures, however, can not be as closely controlled as in the phytotron and vary considerably throughout the year, from 10°C-35°C. The roof location and northerly orientation of the glasshouse makes maximum use of natural daylight. Fluorescent lamps were used to extend the photoperiod to sixteen hours. Relative humidity was not controlled. The artificially-lit LBH cabinets available within the Forestry Department were similar to those at CERES.

3.2.2 Apparatus for Controlling Soil Temperature

The system used for controlling soil temperature in the air-soil temperature experiments is illustrated in Figure 3.1. Soil temperatures, independent of the cabinet air temperatures were maintained by means of water-filled tanks inside the LB cabinets. Each insulated tank (117 cm long x 29 cm wide x 29 cm deep - inside measure) was fitted with eight free-draining copper pots (14.8 cm diameter x 20.5 cm height) coated inside with a non-toxic plasticised asphalic compound.

Soil temperatures below the ambient air temperatures were obtained by circulating a brine of water-diluted glycol antifreeze from a refrigerated water-bath through the copper pipes along the bottom of each tank. The flow of brine was regulated by a manifold system mounted between two tanks.

Thermostatically controlled heating (Thermomix II -B.Braun Melsungen) maintained each water tank at the desired temperature, with an accuracy of ± 0.25°C. Continuous stirring (thermomixes) avoided temperature gradients developing within the tanks. Copper constantan thermocouples placed near the centre of the tanks and connected to a

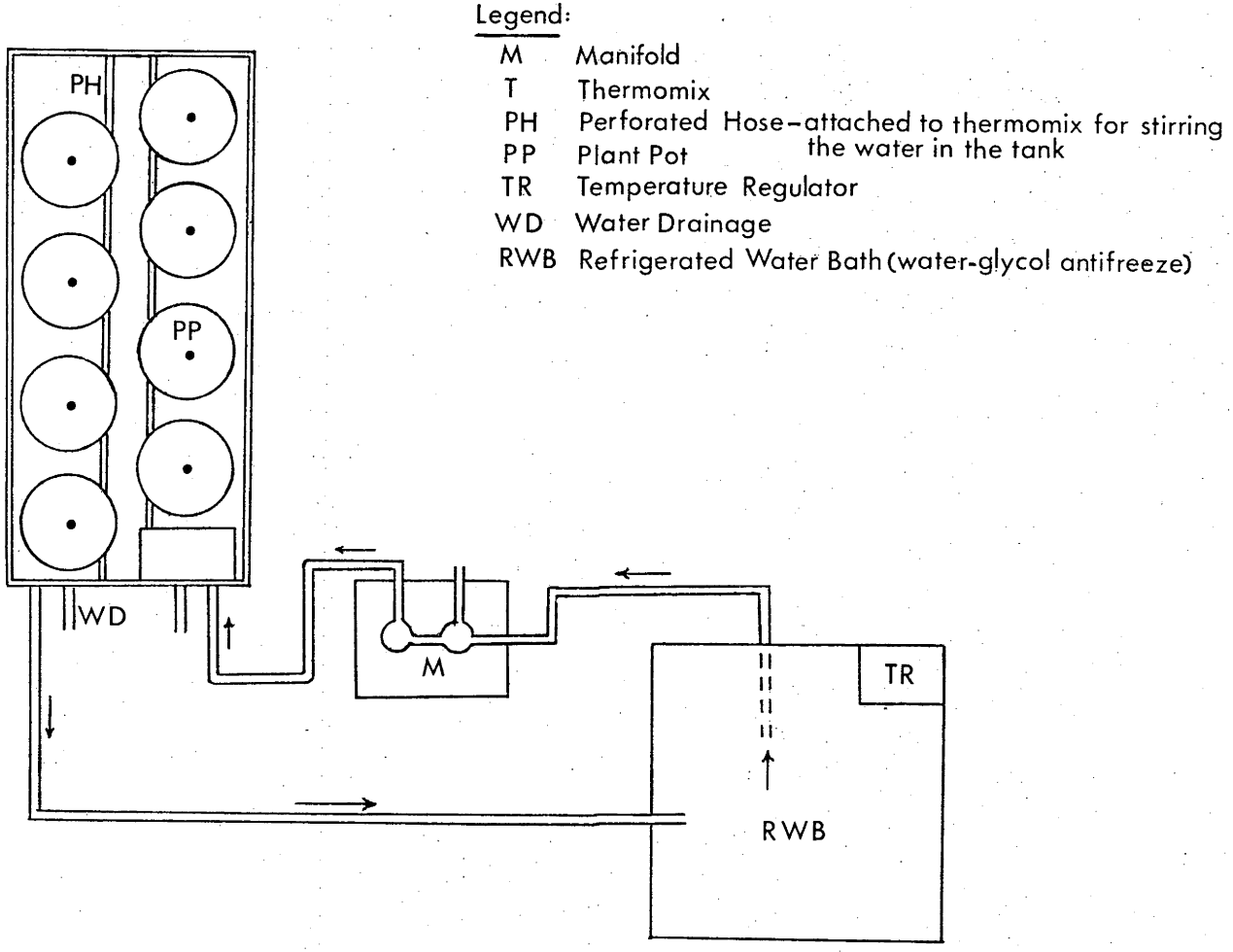


Figure 3.1. The system used for controlling soil temperature.

Honeywell multichannel potentiometric recorder, monitered the tank water temperatures continuously. Actual soil temperatures were not constantly monitered. Dry bulb thermometers placed at various positions in the pots were checked from time to time and these showed soil temperature differences did not differ more than ± 0.5°C from the desired temperature.

3.2.3 Apparatus for Measuring Photosynthesis and Respiration

The infra-red gas analyser (IRGA) used for measuring photosynthesis and dark respiration was a Grubb Parsons, England, Model SB2. The gas circuit was an open system, as illustrated in Figure 3.2. Air was drawn into the system from the roof of the building. To eliminate any CO_2 concentration gradients and to smooth any oscillations in the flow rate due to the pump, the air was stirred in a large drum. The air coming from the drum was then divided into two streams. One was taken as the reference air sample to the gas analyser, the other to the assimilation chamber. The flow rate of the gas stream through the chamber was regulated by a 'Flostat' regulator. Flow rates of 10-12 l/min were used. Flow rates of the gas stream, i.e., entering and leaving the assimilation chamber and entering the IRGA, were checked with 'Gapmeter' flowmeters. The air returning from the assimilation chamber was passed through a water bath maintained at room temperature and a small portion of the air flowed to the IRGA as the sample air. Excess air was exhausted to the atmosphere. Both sample and reference air were dried by passing through calcium chloride columns before entering the IRGA.

The IRGA was calibrated to measure the CO_2 differential against a background of 200 p.p.m. CO_2 in nitrogen. Attached to the IRGA was a range regulator with which the scale could be set to read zero, photosynthesis or respiration. During measurement, the IRGA reading was displayed on a Heath Servo Recorder (Model EUW-20A). This was used in deciding the point at which photosynthesis or respiration was stable before the final reading was taken.

The assimilation chamber, made of clear perspex (30.0 cm x 28.0 cm x 50.5 cm) was situated inside an artificially-lit LB cabinet (see section 3.2.1). Air was introduced near the top of the assimilation chamber and exhausted near the base. Adequate stirring of air by a fan, eliminated CO_2, O_2 and H_2O vapour gradients and ensured temperature uniformity.

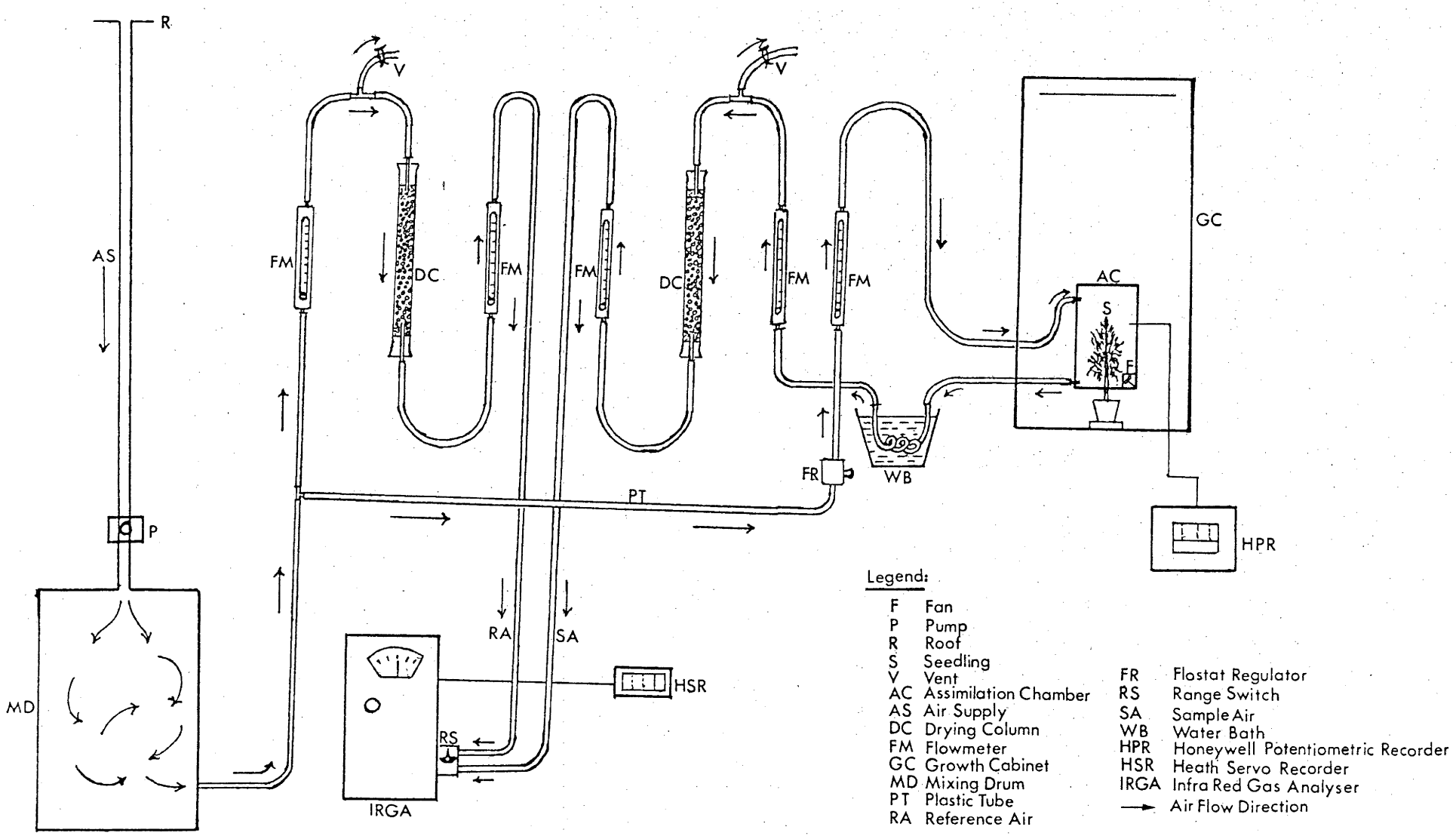


Figure 3.2 Apparatus for measuring net photosynthesis and respiration.

Air temperatures within the chamber were regulated by adjusting the temperature controller of the LB cabinet. Temperatures were monitored by a copper constantan thermocouple connected to a Honeywell multi-channel potentiometric recorder. The LB cabinet provided light intensity up to 835$\mu Em^{-2}sec^{-1}$ (4000 f.c.). During measurement only the shoot portion of the seedling was enclosed in the assimilation chamber. This was made possible by a removable, two-segmented disc, with a 2 cm hole in the centre which was fitted to the bottom of the chamber. Modelling clay was used to make an air-tight seal around the stem.

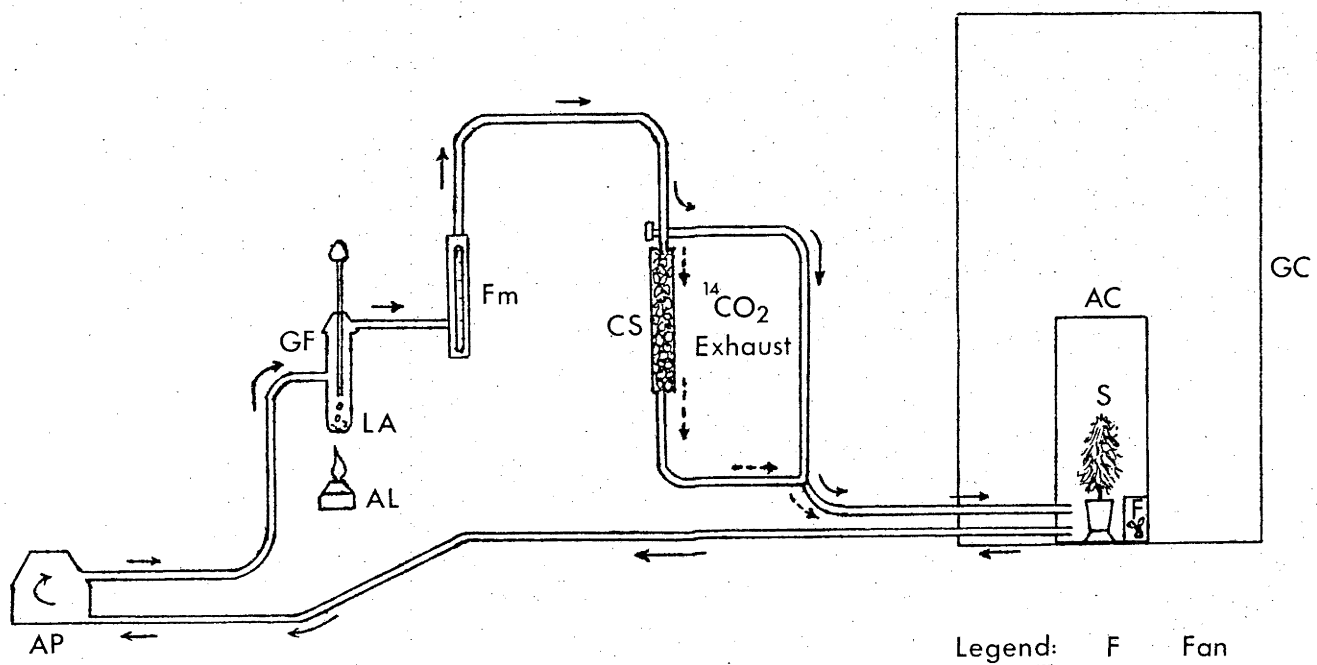
When required, root temperatures were maintained by wrapping the seedling container with towels soaked at the required temperature. When placed in an 18 cm polyfoam pot, this adequately maintained the desired temperature for the measurement period.

3.2.4 Apparatus for Feeding $^{14}CO_2$ and Assay of ^{14}C Radioactivity

The seedlings were fed $^{14}CO_2$ in a closed system as illustrated in Figure 3.3. Each seedling received 5μCi of aqueous Sodium [^{14}C] Carbonate (specific activity 1.0mCi/mmol or 5.0mCi/mmol). $^{14}CO_2$ was generated by heating sodium carbonate and a few ml of 88% lactic acid in a generating flask. The $^{14}CO_2$ was then pumped into the assimilation chamber by a circulation of air, at the rate of 4l.min^{-1} for ten minutes.

Before generating $^{14}CO_2$ a potted seedling was introduced into the assimilation chamber. The clear perspex chamber (16.5 cm x 26.5 cm x 61.0 cm height) was equipped with a fan for mixing the $^{14}CO_2$. The chamber was situated in an LB cabinet (Morse and Evans, 1962), the temperature and light intensity was adjusted to match the growing conditions of the seedlings. The actual temperature in the assimilation chamber was not monitored.

Plant parts to be assayed were oven-dried and weighed. Larger plant parts were ground through a 1mm mesh with a Wiley Mill (standard model). A Wiley laboratory mill, Micromodel, 40 mesh was used to grind the smaller material. One sample from each seedling component was assayed using the method described by O'Brien and Wardlaw (1961). A 30 mg (or less) sample of powder was placed into an aluminum planchet (1 cm diameter aperture) and counted for radioactivity. A Tracerlab-Omni/Guard Scaler, Model SC520M, with a thin window gas flow G.M. tube, counted the radioactivity of each sample for a five minute period.



Legend:

F	Fan
S	Seedling
AC	Assimilation Chamber
AL	Alcohol Lamp
AP	Air Circulating Pump
Fm	Flowmeter
GC	Growth Cabinet
GF	Generating Flask
LA	Lactic Acid
CS	Caustic Soda
⟶	Air Flow Direction

Figure 3.3. Closed system used in feeding seedlings $^{14}CO_2$.

Corrections for background were made.

3.3 GENERAL EXPERIMENTAL PROCEDURES

3.3.1 Raising Seedlings

To obtain uniform germination *P. radiata* seeds were soaked in distilled water and refrigerated for two to three days prior to sowing. Seeds were sown in germination trays filled with a 1:1 perlite and vermiculite mixture. To prevent any possible damage to the developing rootlets tap water only was applied until the seedling cotyledons had fully emerged.

The seedlings were transplanted three to four weeks after sowing, when lateral rootlet and primary leaf development was evident. Root damage during transplanting was minimized by flooding the seed trays with water before carefully removing the seedlings. Only healthy seedlings with well-developed, undamaged root systems and shoots were potted in 13 cm or 15 cm pots with a moist 1:1 perlite: vermiculite mixture. More than the required number of seedlings were transplanted, to allow for mortality and further selection for uniformity of size before the actual treatments.

Experimental stock was raised in either the controlled environments at CERES or the Forestry Department glasshouse. For some experiments, department raised stock was transferred for use at CERES.

3.3.2 Selection of Seedlings for Experiments

The selection procedure adopted for all experiments includes the following steps. Seedlings were first culled from the potted stock on the basis of visible morphological shoot abnormalities, e.g., double leaders, deformed stem, discolouration. From the remaining seedlings, a predetermined number with the most uniform stem diameters and heights and to a certain extent, size of root system were chosen for the experiments. Even with a large number of seedlings to chose from, uniformity in size of root system as well as uniformity in shoot size was most difficult to achieve. The physical limitations of space and the laborious task involved in assessing root regeneration potential limited the sample size used.

3.3.3 Maintenance of Seedlings

Seedlings for most treatments, once transplanted were watered twice daily. At CERES a modified Hoagland nutrient solution (see Appendix I) was added in the morning and tap water in the afternoon. Seedlings under high temperature regimes, e.g., 30°/25°C, were given an additional mid-day application of tap water. At the Forestry Department, seedlings were given tap water twice daily. A diluted Aquasol nutrient solution was applied weekly. Where nutrient supply was to be controlled demineralized, de-ionized or distilled water was used in place of tap water.

Root exposure resulting from washing out of planting medium during watering was checked throughout the growing period prior to and after treatment. Whenever possible, seedlings were shifted periodically to minimize any position effects in the glasshouse or cabinet.

3.3.4 Method of Root-Pruning and -Trimming for RRP Assessment

The method adopted for pruning and trimming a seedling root system to ascertain its root regenerating potential (RRP) was a modification of the technique evolved by Stone and co-workers (Stone, 1955, 1966, 1967a; Stone and Schubert, 1959a, 1959b; Stone and Benseler, 1962; Stone *et al.*, 1962, 1963; Krugman and Stone, 1966; Stone and Jenkinson, 1971). It involved the following procedures. Seedlings were removed from the pots and the root systems washed free of planting media. The roots were carefully extended and pruned at a specified length from the cotyledons, usually 21 cm. All white root tips, unless specified otherwise, were pinched off with forceps. Broken, pruned and trimmed roots were retained when estimates of total root removed were required. The root systems were kept moist with running water at all times. Exposure was kept to as short a period of time as possible. However, this was largely dependent upon the number of actively growing roots on the root system.

The seedlings were then replanted into a moist 1:1 perlite and vermiculite mixture and placed into the treatment for a specified length of time.

3.3.5 Harvesting Seedlings

Seedlings were harvested three to four weeks after root-pruning and -trimming in most experiments. At most harvests, stem diameter and height were remeasured. Gas exchange, internal moisture stress, relative turgidity and stomatal resistance were also measured at this time in some experiments.

After all measurements were made, the seedling stem was cut 10 cm below the cotyledons and placed in a bag for drying. For translocation studies the shoot was separated into stem and branch components. Further separation of live needles or needle portions from those dead or partially desiccated was required for gas exchange estimates.

The root system was immersed in water and carefully washed free of growing media. The number and length of all new white roots were measured, except in experiments where only roots above specified lengths were measured.

Root regeneration potential (RRP) of the seedlings was based on the total number and length of new white roots produced. Further separation into the total number of short roots (SR) and long roots (LR) was made, with the lengths delineating short and long roots specified in each experiment.

Differentiation between lateral root initiation potential and lateral root elongation potential, together referred to as RRP by Stone and Benseler (1962) and Stone *et al.* (1962) was not made. This was largely due to the fact that the origin of all the new root growth could not be readily determined in all treatments. At high temperatures especially, rapid suberization of new roots even after three weeks made it difficult to determine which roots were newly regenerated, let alone which were newly elongated or initiated.

The root and shoot components were oven dried in a forced-air oven at 80^{o}F for at least 48 hours before weighing.

3.4 GENERAL PLANT PARAMETERS MEASURED

The parameters measured in all experiments are discussed in this section. Those parameters specific to some experiments are discussed in the relevant sections.

(i) Stem diameter was measured 10 mm below the cotyledons. The area was inked for consistency in the initial and final measurements. Three vernier caliper readings were taken around and at right angles to the stem and their average recorded as the stem diameter. Measurement was made in mm to the nearest two decimal places.

(ii) Stem height was measured as the distance from the cotyledons to the approximated apex. Minimal handling was required to avoid damage to the delicate apex. Unavoidably, this measurement was subjective but reasonably consistent estimates were obtained with practice. Measurement was made in cm to the nearest two decimal places.

(iii) Root regeneration potential was assessed by measurement of a number of root parameters including the following:

SR: the total number of newly regenerated short white roots per seedling. Short roots were defined as roots below a certain specified length, the length chosen varied with experiment.

LR: the total number of newly regenerated long white roots per seedling. Long roots were defined as roots above a certain specified length, the length chosen varied with experiment.

GT: the total number of newly regenerated white roots per seedling.

TL: the total length of newly regenerated white roots per seedling. In some experiments, only those roots above a certain length were measured, this length varied with experiment. Measurement was made in cm to the nearest one decimal place.

(iv) Dry weights of seedling parts were determined after oven-drying the material for at least 48 hours. Before weighing, the material was cooled to room temperature in desiccators. The seedling parts generally included: a) the various components of the shoot, i.e., branches, stems, needles - both green and dead, and b) various components of the root, i.e., newly regenerated roots, residual root. Measurement was made in grams to the nearest two or three decimal places. Root:shoot ratios of seedlings were determined on a dry weight basis.

3.5 CALCULATIONS AND ANALYSIS

3.5.1 Calculations

(1) Mean relative growth rates of diameter and height were calculated in most experiments, using the formula discussed by Radford (1967), Šesták, Čatský and Jarvis (1971) and Ledig (1974). The calculation was as follows: Mean relative growth rate (RGR)

$$= \frac{\ln X_2 - \ln X_1}{t_2 - t_1}$$

where X_2 = diameter, height at time t_2

X_1 = diameter, height at time t_1

t_1 and t_2 are times of initial and final measurement respectively.

(2) The rate of CO_2 exchange, photosynthesis and dark respiration, was calculated using the following formula:

$$\text{Net Photosynthetic Rate (mg/g/hr)} = \frac{\Delta R \times F \times 44 \times 273 \times P \times 60 \times 10^3}{g \times 22.414 \times T \times 1013 \times 10^6}$$

where ΔR = the difference in CO_2 concentration of the air streams before and after the assimilation chamber measured at the same temperature and pressure in p.p.m.

F = air flow rate through the assimilation chamber in l/min.

T = both the temperature (^oK) at which the flowmeter was calibrated and the temperature of the flowmeter at the time of observation. They were the same as room temperature.

P = barometric pressure (mb) at the time of observation, usually the same as normal atmospheric pressure and for all calculations taken as 1013 mb.

g = dry weight of needles in grams. Unless stated, only green needles were used in the determination.

(3) In the translocation work, the radioactivity or ^{14}C concentration of each plant part was expressed as counts per minute (CPM) per gram dry weight. The amount of photoassimilated ^{14}C accumulated in each plant part was expressed as a percentage of the total plant ^{14}C recovery (see Wardlaw, 1965). A relative thickness curve (I.F. Wardlaw, pers. comm.) of count rate plotted against increasing powder thickness (powder weight) was prepared for the root

(Appendix II). The curve provided suitable corrections for powder samples less than the standard 30 mg.

3.5.2 Analysis of Data

Duncan's multiple range test (Steele and Torrie, 1960, pp.107-109) or Student's t-test (Snedecor and Cochran, 1967, pp.103, 114-116) were used for the comparison of treatment means in most experiments. The Duncan's test was used to compare means more than two in number.

Coefficients of variability were calculated in the earlier experiments to indicate the amount of variation in the samples. All percentage data was transformed into their arcsin values for analysis. Computation was carried out using programmes from the SPSS manual (Statistical Package for the Social Sciences) by Nie *et al.* (1972).

CHAPTER 4

THE EFFECTS OF SOIL NUTRIENT STATUS ON ROOT REGENERATION POTENTIAL AND SHOOT GROWTH OF *Pinus radiata* SEEDLINGS

4.1 INTRODUCTION

In Australia, the more fertile soils have generally been cleared for agriculture and forestry activity has been frequently relegated to topographically difficult or infertile sites (Brown and Hall, 1968; Florence, 1969; Shepherd, 1971). Forest plantations, therefore, must often be established on poor soils low in total P and lacking in micronutrients Ca, Co, Zn, Cu, Mo (Friedel, 1972; Ruiter, 1972); on soils of high Al availability (Humphreys and Truman, 1972), or on soils deficient in K (Raupach and Clarke, 1972) and B (Will *et al.*, 1963; Stone and Will, 1965b; Gentle, pers. comm.; Snowdon, 1972).

Of the major elements essential for seedling growth, P deficiency appears to be the most important in Australian (Stoate, 1950; Kanwar, 1959; Tamm, 1964; Raupauch, 1967; Hopkins, 1971a; Friedel, 1972; Ruiter, 1972) and New Zealand soils (Weston, 1956; Tamm, 1964; Will, 1965; Mead, 1966; McKinnon, 1969; Levy and St. John, 1974; Berg, 1975). Nitrogen deficiency has also been recognized and has been closely studied in relation to plantation establishment and management procedures (Appleton and Snow, 1966; Waring, 1972) including its significance in the establishment of successive rotations of forest crops (Lewis and Harding, 1963; Waring, 1963; Stone and Will, 1965a; Florence and Lamb, 1971).

The mineral requirements of *P. radiata* have been determined (Smith, 1943; Will, 1961, 1965; Humphreys and Truman, 1964; Raupauch, 1967) and the effects of various element deficiencies on growth have been described (Ludbrook, 1940; Smith, 1943; Stoate, 1950; Purnell, 1958; Kanwar, 1959; Lewis and Harding, 1963; Will, 1961, 1965; Stone and Will, 1965b). Nutrient deficiencies have been shown to have different effects on the growth of seedling parts. Will (1961) found that N and P deficiencies stimulated root growth and reduced shoot growth in *P. radiata* seedlings. Similarly, better root development was found by Purnell (1958) in P deficient treatments. Shoot growth, however, was not reduced but resembled that of seedlings grown in full

nutrient. The availability of both N and P immediately after planting and throughout the first growing season appears to be important in determining maximum early growth in *P. radiata* seedlings. Significant growth responses have been obtained following application of these major elements (Lewis and Harding, 1963; Waring, 1963, 1969, 1971 ; Will, 1964; Wds. For. Dept., S.A., 1969, 1970; Brown and Hall, 1968; For. Tim. Bur., 1972; Berg, 1975; Woods, 1976). However, it has not been previously determined to what extent soil nutrient deficiencies do affect root growth responses in *P. radiata* during the critical period following planting. Three nutrient studies are described in this chapter. The main objective of the first two, was to examine the effects of N and P deficiencies on the root regeneration potential of *P. radiata* seedlings. The effects of a combined NP deficiency was examined in the first experiment and the effects of N and P deficiency separately in the second.

As indicated in Chapter 1 (Section 1.2.2) seedling nutritional status and indirectly nutritional status of the nursery soil influence survival and early growth of newly transplanted seedlings. Newly transplanted seedlings of *P. radiata* (Woods, 1976) and *Picea abies* (L.) Karst. (Machek, 1972/1973) for example, have shown improved field performance in relation to the fertility of the soil in which they were grown. Seedling survival and height growth after transplanting may increase with improved nursery fertility (Smith *et al.*, 1966; Benzian and Freeman, 1967; Machek, 1972/1973; Woods, 1976) but the effect of this fertility on immediate growth response, that is, root regeneration potential has not been determined. In the field, it is difficult to ascertain whether nutrient application at the time of or after planting is more important to seedling field performance than is nursery soil fertility. However, it is recognized that any factor which inhibits root regeneration potential in seedlings will reduce the chances of survival and maximum early growth. The aim of the third experiment was, therefore, to examine the root regeneration potential of both nutrient 'starved' *P. radiata* seedlings and seedlings supplied with ample nutrients to determine the effect of seedling nutrient deficiencies at the time of planting on subsequent root regeneration potential.

4.2 MATERIALS AND METHODS

P. radiata seeds (Grade 1) from Green Hills S.F., N.S.W. were sown in the Forestry Department glasshouse and the seedlings raised as described in Chapter 3 (Section 3.3.1). Except for experiment 3, nutrient and water applications prior to treatment were as described in Chapter 3 (Section 3.3.3).

In the first experiment seedlings of approximately 150-250 mm in height were transferred to an LBH growth cabinet (described in Chapter 3, Section 3.2.1) for an eleven day acclimation period prior to treatment. The day/night air temperature of the cabinet was set at $21^{o}/11^{o}C$ with a sixteen hour day and an eight hour night. A cool air temperature was chosen to simulate the temperature conditions encountered in the forest at the time of planting. Light intensity at plant height was approximately $575\mu E.m^{-2}.sec^{-1}$ (3000 f.c.) and relative humidity was above forty per cent. Nine seedlings of uniform diameter and height were chosen for each treatment. The root system of each seedling was thoroughly washed in de-ionized water and pruned to 30 cm from the cotyledons. All remaining white root tips $\geq$ 0.25 cm were pinched off (detailed in Chapter 3, Section 3.3.4).

The seedlings were grown under either a full (Full) or a minus nitrogen and phosphorus (-NP) nutrient regime for four weeks. Nutrient solutions (see Appendix III) were applied every second day, de-ionized water on the others. Only one morning application of nutrient or water was necessary to keep the planting media moist due to the cool air temperatures and reduced absorption surface of the seedling root system. Once a week, the seedlings were excessively watered (de-ionized) to flush out any accumulation of nutrients that may have developed.

After four weeks the seedlings were harvested. Root regeneration potential, final shoot and total root dry weights, and root:shoot ratio were determined for each seedling as described in Chapter 3 (section 3.4). Root regeneration potential (RRP) was based on the number of new white roots $\geq$ 1.25 cm (GT), the number of new white roots $\geq$ 2.5 cm or long roots (LR), the number of new white roots 1.25-2.4 cm(SR) or short roots and the total length of LR (TL). Morphological differences in both the shoot and root were evaluated visually.

In the second experiment seedlings of 200-250 mm in height were moved to CERES phytotron. After fumigation with organo phosphorus a standard entry procedure, the seedlings were placed in a glasshouse (as described in Chapter 3, Section 3.2.1) with a day/night air temperature of $15^{o}/10^{o}C$. As in Experiment 1, a cooler air temperature was chosen to simulate the temperature conditions encountered at the time of planting.

After an acclimation period of ten days, fifteen seedlings were selected for treatment. Seedling root systems were thoroughly washed with demineralized water, pruned to 30 cm from the cotyledons and all white root tips $\geq$ 0.25 cm pinched off. Five seedlings were grown under each of the following nutrient regimes: full nutrient (Full), minus nitrogen (-N) and minus phosphorous (-P). Nutrient solutions (see Appendix III) were applied every second day. On the other days, demineralized water was given. Pots were flushed weekly with demineralized water to avoid nutrient accumulation.

After four weeks of treatment the seedlings were harvested. Root regeneration potential, final shoot and total root dry weights, and diameter and height increments were determined as described in Chapter 3 (Sections 3.4, 3.5). As in Experiment 1, the number of new white roots $\geq$ 1.25 (GT), the number of new roots $\geq$ 2.5 cm (LR) and the total length (TL) of LR were measured for each seedling. The number of new roots 1.25-2.4 cm or short roots (SR) was also determined. Morphological differences in the shoot and root were evaluated visually.

In the third experiment seedlings were transplanted four weeks after germination and twenty plants each were raised under either a full nutrient or a no nutrient regime. Seedlings under the full nutrient (Full) regime were given nutrients (see Appendix III) every second day and de-ionized water every other day. All pots were flushed weekly with de-ionized water. Glasshouse air temperatures were kept above $20^{o}C$ during the treatment period. Day-length was extended to sixteen hours with flourescent lamps.

After three months, six of the most uniform seedlings were chosen from each nutrient regime. By this time, differences in seedling size between treatments were quite pronounced. Growth in seedlings under the No nutrient regime was stunted. Chlorosis especially in the lower needles, reddening of the cotyledons and short needles were typical symptoms noted. The seedlings grown in the Full regime, on

the other hand, were healthy with no nutrient deficiency symptoms.

The root systems of the selected seedlngs were pruned to 25 cm from the cotyledons and all remaining white root tips pinched off. All seedlings were placed under a Full nutrient regime, the same as used before root-pruning.

After twenty-four days, all seedlings were harvested. Root regeneration potential, final shoot and total root dry weights, and diameter and height increments were determined as described in Chapter 3 (Sections 3.4, 3.5.1). Root regeneration potential was based on the number of new white roots $\geq$ 0.5 cm (GT), $\geq$ 1.5 cm (LR), 0.5-1.4 cm (SR) and the total length (TL) of LR, produced by each seedling. Because seedlings in this experiment produced much shorter new white roots compared to those produced by seedlings in Experiments 1 and 2, shorter lengths were used to designate the LR and SR.

4.3 STATISTICAL ANALYSIS

A t-test for group data was used to test for significant differences between the treatment means for each parameter in Experiments 1 and 3.

In Experiment 2, differences between treatment means of each parameter were compared using Duncan's multiple range test at the 5% level of significance. Coefficients of variability were calculated for all parameters in each experiment. Results of the analyses of Experiment 1 and 2 are presented in Table 4.1. Results of analysis of Experiment 3 are presented in Table 4.2.

4.4 RESULTS

4.4.1 Experiment 1

4.4.1.1 Root Regeneration Potential

The nutrient regimes had no significant effect on the total number of new roots (GT) or on the number of short roots (SR) produced (Table 4.1). Differences in both the number of roots $\geq$ 2.5 cm (LR) and total length of roots $\geq$ 2.5 cm (TL), however, were significant between treatments. As shown in Table 4.1 seedlings in the -NP treatment produced an average of 18 long roots with a TL of 71.4 cm compared to those in Full which produced only 11 long roots with a TL of only

Table 4.1 Effects of nutrient deficiencies on shoot growth and root regeneration potential of *P. radiata* seedlings.

Parameter	Experiment 1			Experiment 2	
	treatment mean[1]	(C.V.)[2]		treatment mean[1]	(C.V.)[2]
Root Regeneration					
Number of new roots ≥1.25 cm (GT)	FULL -NP	32(43.0) 40(37.8)	NS	-N FULL -P	138(35.2) 256(40.2) 377(57.6)
Number of new roots ≥2.5 cm (LR)	FULL -NP	11(27.2) 18(44.6)	**	-N FULL -P	31(90.7) 57(65.6) 71(50.5)
Number of new roots 1.25-2.4 cm (SR)	FULL -NP	21(55.8) 22(54.11)	NS	-N FULL -P	107(34.1) 199(43.6) 302(64.3)
Length of new roots ≥2.5 cm in cm (TL)	FULL -NP	38.5(46.6) 71.4(29.7)	**	-N FULL -P	124.(89.2) 230.(70.4) 280.(85.0)
Diameter and Height					
Initial diameter (mm)	FULL -NP	2.9(9.3) 2.9(11.0)	NS	-N FULL -P	4.2(26.2) 4.6(18.6) 4.9(24.0)
Diameter increment (mm)	not measured			FULL -P -N	0.7(38.0) 0.7(57.1) 0.8(44.2)
Initial height (cm)	FULL -NP	15.5(10.0) 15.9(11.3)	NS	-N -P FULL	21.9(31.3) 24.1(31.3) 24.4(27.0)
Height increment (cm)	not measured			FULL -P -N	1.3(70.8) 1.9(75.7) 2.2(86.8)
Final Dry Weight					
Shoot (g)	FULL -NP	1.10(27.8) 1.20(28.9)	NS	-N FULL -P	4.89(72.2) 6.64(65.0) 8.85(60.5)

(Cont'd next page)

Table 4.1 (Cont'd)

Parameter	Experiment 1		Experiment 2	
	treatment	mean[1] (C.V.)[2]	treatment	mean[1] (C.V.)[2]
Total root (g)	FULL	0.42(18.3)	-N	1.22(47.7)
	-NP	0.47(18.3) NS	FULL	2.14(53.8)
			-P	2.44(57.0)
Root:shoot ratio	FULL	0.39(13.4)	-P	0.23(9.6)
	-NP	0.41(17.0) NS	-N	0.25(27.4)
			FULL	0.26(11.3)

1 Mean of 9 replicates (Experiment 1), 5 replicates (Experiment 2).

2 C.V. = Coefficient of Variability in per cent.

Note: In Experiment 1, differences between treatment means are significant at * $P<0.05$, ** $P<0.01$ or NS non significant (Student's t-test).

In Experiment 2, vertical lines join treatment means which are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

38.5 cm, almost half the total length of roots produced in the -NP nutrient treatment. Coefficients of variability were high for all root parameters measured in both treatments but this did not swamp the real differences observed in root production between the treatments. The number of replications, only nine each, was low so that more extensive testing could be expected to reduce the variability but probably not the real difference between the treatments.

4.4.1.2 Final Dry weights

No significant differences were found in the shoot and root dry weights or root:shoot ratios between treatments. Variability in final dry weights was less than in root parameters measured.

4.4.1.3 Morphological Differences in Shoot and Root

a) Shoot

Seedlings in both Full and -NP treatments at the end of the three week post root-pruning period showed distinct visual symptoms of nutrient deficiency in the foliage. Chlorosis was evident in the apical needles and lateral branches and at the base of secondary needle fascicles of most seedlings. Similar change in colour has been observed in the foliage of seedlings undercut in the nursery (Ruiter, pers. comm.) which may be due to N, P and K being translocated to the root for root extension. Some seedlings in the -NP treatment had foliage of a blue-green tinge near the terminal apex.

Apical needles were much longer and lateral branch growth more pronounced in the Full treatment than in -NP. Little or no growth was evident in the lateral branches of seedlings in the -NP treatment.

Two to three days after root-pruning and -trimming, needle desiccation was noted in all re-planted seedlings in both treatments. After one week almost all the primary needles, with the exception of those closest to the apices were completely dry. Secondary needles, however, suffered only partial dieback which started from the tip and extended a certain distance towards the base of the needle. The extent of dieback in the needles varied among seedlings. Similar desiccation occurred in all three experiments and could probably be attributed to the root-pruning and -trimming of the seedlings. Higher rates of transpiration compared to absorption, the result of a reduced absorption surface in the roots, probably led to an increasing moisture stress

within the seedlings. Areas of lowest moisture content, that is, the mature primary needles and extremities of secondary needles were first to suffer from the internal moisture imbalance. Needle desiccation and internal moisture stress in seedlings following root-pruning and -trimming are dealt with to a greater extent in Chapter 9.

b) Root

Seedlings in the Full treatment produced comparatively thicker roots than in -NP, however, not all seedlings showed these differences.

4.4.2 Experiment 2

4.4.2.1 Root Regeneration Potential

The nutrient regimes had a significant effect on the number of new white roots 1.25-2.4 cm (SR) and the total number of new white roots produced (GT). Table 4.1 shows that SR and GT were significantly greater in -P treatment than in -N, but there was no significant difference between -N and Full or -P and Full treatments. The -P treatment produced 302 SR compared to 107 in the -N treatment. Likewise, the -P treatment produced a total number of 377 new white roots (GT) compared to only 138 in the -N treatment.

No significant differences were found in the number of new long roots ($\geq$ 2.5 cm) produced despite the great differences in the actual mean values between treatments. Variability in the number (LR) and total length (TL) of new long white roots produced by seedlings was very high. In the -N treatment for example, coefficients of variability were 90.7% for LR and 89.2% for TL. The number of replicates, only five per treatment, was low and such variability could account for the differences in treatment means being non significant.

4.4.2.2 Final Dry Weight

The different treatments had no significant effect on the shoot and total root dry weights or root:shoot ratios of the seedlings. Mean total root dry weights in -N was 1.22 g and in -P 2.44 g, but the difference was not significant. Again, small sample size and high variability would mask any possible treatment differences.

4.4.2.3 Diameter and Height Growth

No significant differences were found between treatments in diameter and height increment. Mean height increments of 1.28, 1.94 and 2.16 cm were measured in Full, -P and -N treatments respectively, but were not significantly different. As shown in Table 4.1, variability in height increment was high.

4.4.2.4 Morphological Differences in Shoot and Root

a) Shoot

In both Full and -P treatments most seedlings developed terminal resting buds. All new needles produced after transplanting were shorter than those produced prior to treatment. Chlorosis was evident in seedlings of each treatment, especially in the apices. Needle desiccation as described in section 4.4.1.3(a) occurred in all seedlings.

b) Root

Seedlings in all treatments produced numerous short, fine to thick roots and relatively few long ones. Differences observed in the morphology of new white roots were not distinct between treatments.

4.4.3 Experiment 3

4.4.3.1 Root Regeneration Potential

The nutrient regime in which seedlings were grown prior to root-pruning had a significant effect on the numbers (GT, LR, SR) and total length of LR (TL) produced during the four weeks after pruning. Table 4.2 shows the differences between treatments, with superior performance shown by the seedlings from the Full nutrient regime. Variability in these parameters was high.

4.4.3.2 Final Dry Weights

Significant differences between treatments were found in final shoot and total root dry weights and root:shoot ratios, but the initial diameter and height of seedlings grown with Full nutrient was much greater than that of seedlings grown with No nutrients.

Table 4.2 Effect of nutrient deficiency on shoot growth and root regeneration potential of *P. radiata* seedlings (Experiment 3).

Parameter	Experiment 3		
	treatment mean[1] (C.V.)[2]		
Root Regeneration			
Number of new roots ≥0.5 cm (GT)	NO FULL	11(16.3) 127(40.7)	**
Number of new roots 0.5-1.24 cm (SR)	NO FULL	6(31.2) 102(37.2)	**
Number of new roots ≥1.25 cm (LR)	NO FULL	5(71.0) 25(24.1)	*
Length of new roots ≥1.25 cm in cm (TL)	NO FULL	16.6(60.6) 71.3(66.0)	*
Diameter and Height			
Initial diameter (mm)	NO FULL	1.8(7.9) 3.1(11.2)	**
Diameter increment (mm)	NO FULL	0.1(62.5) 0.2(88.0)	NS
Initial height (cm)	NO FULL	4.3(30.2) 17.1(20.8)	**
Height increment (cm)	NO FULL	0.7(9.0) 1.4(1.4)	*
Final Dry Weight			
Shoot (g)	NO FULL	0.18(32.0) 1.30(24.6)	*
Total root (g)	NO FULL	0.15(29.2) 0.40(28.5)	**
Root:shoot ratio	FULL NO	0.28(17.2) 0.76(14.2)	*

1 Mean of 6 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Differences between treatment means are significant at * $P<0.05$ ** $P<0.01$ or NS non significant.

4.4.3.3 Diameter and Height Growth

The Full nutrient regime had a significant effect on seedling diameter and height growth prior to and after transplanting. The differences in initial diameter and height between treatments were significant prior to root-pruning and -trimming. Seedlings in Full nutrient had a mean initial diameter of 3.1 mm and height of 17.1 cm compared to a mean initial diameter of 1.8 mm and height of 4.3 cm for seedlings grown with no nutrients. Height increments of seedlings grown in the two treatments were significantly different. Height growth in seedlings from the Full nutrient regime was 1.4 cm compared to only 0.7 cm in the No nutrient regime, one half of that produced by seedlings from the Full regime.

4.5 SUMMARY OF RESULTS

4.5.1 Experiment 1

(i) Seedlings planted into a minus nitrogen-phosphorous regime (-NP) produced a significantly greater number (LR) and total length (TL) of new white roots $\geq$ 2.5 cm compared with seedlings in the Full nutrient treatment.

(ii) Final dry weights of shoot and total root, and root:shoot ratios were not significantly different between treatments.

4.5.2 Experiment 2

(i) Deficiencies in N and P separately had no significant effect on LR and TL. Significant differences were found between treatments in the number of new white roots 1.25-2.4 cm (SR) and the total number of new white roots $\geq$ 1.25 cm (GT). Seedlings in the -P treatment produced significantly higher SR and GT than seedlings in the N deficient treatment.

(ii) Diameter and height increments, final dry weights of shoot and total root, and root:shoot ratios were not significantly different between treatments.

4.5.3 Experiment 3

(i) Seedlings raised with no added nutrients were considerably smaller in diameter and height than seedlings with full nutrient and showed symptoms of nutrient deficiency.

(ii) Once transplanted, seedlings raised under full nutrient, showed significantly greater response in terms of root growth than those seedlings raised with no nutrients.

(iii) Height increment was greater in seedlings raised under full nutrient but there were no differences in diameter increment between those seedlings raised under the Full or No nutrient regimes.

(iv) Final dry weights of shoot and total root were significantly greater for seedlings raised under full nutrient. Seedlings raised with no nutrients had a significantly greater root:shoot ratio.

4.6 DISCUSSION

The results indicate that root regeneration potential (RRP) and shoot growth of newly transplanted *P. radiata* seedlings are not significantly affected immediately by the nutritional status of the planting medium into which the seedlings are transplanted. The nutritional status of the medium in which the seedlings are raised, however, will influence significantly both shoot and root growth of seedlings prior to and immediately after transplanting (Experiment 3).

Interestingly, seedlings planted in the absence of two of the most essential elements, N and P, appear to produce the greatest number of long roots (LR and TL). Similar root behaviour has been described in other forest trees by Lyr and Hoffmann(1967). These authors report that in nutrient deficient conditions trees primarily form long "seeking" or "pioneer" roots which explore large volumes of soil in search of nutrients. Deficiency in nitrogen, in particular is known to induce growth in length of roots (Bosemark, 1954; Lundegårdh, 1957 and Meyer, 1963, as cited by Lyr and Hoffmann,1967; Haissig, 1973).

When planted into a N or P deficient condition (Experiment 2), seedlings respond quite differently in terms of root growth than do seedlings in -NP. Seedlings in -P treatment tended to have better root development than those in -N treatment. This is indicated not only by the greater total number of new roots (GT) produced by seedlings in -P,

but the greater number of SR which have the potential to elongate. Significantly lower root growth by seedlings in -N compared to those in -P suggests that an adequate supply of N may be very critical for seedlings at this stage of establishment. The development of roots by seedlings in -P and -N was similar to that reported by Purnell (1958) and Will (1961). These authors observed that P deficiency stimulated the production of longer and better developed roots in seedlings. A decrease in N (in perlite), on the other hand,decreased root growth (Will, 1961).

A deficiency in both N and P stimulated the production of long roots (LR) in seedlings. As a deficiency in N has little effect on root growth, it appears that this increased root length in -NP could be attributed to the absence of P more than of N.

The lack of significant differences between Full nutrient and -N or -P treatments, in all root parameters measured, suggests that the presence of N and P may not be required in the planting medium for regeneration and extension of roots after transplanting. It appears that seedlings are able to mobilize nutrient reserves for at least four weeks, the duration of the present experiments. Nutritional status of the seedlings therefore, may be important in sustaining seedling growth, especially under poor nutrient conditions in the field, until such time as nutrient reserves in the soil can be tapped. Experiments of longer duration are now needed to determine the time period before distinct differences can be observed between nutrient deficient treatments.

There were no significant differences in diameter and height growth between treatments. However, it is interesting to note that although seedlings in -N in Experiment 1 produced the lowest mean values in all the root parameters (see Table 4.1), diameter and height increments were higher than those of the -P and Full treatments. This suggests that under N deficiency shoot growth may be favoured to root growth, due possibly to the ability of seedlings to maintain N in the shoot at the expense of the roots (Will, 1961). Alternatively, under the P deficient treatment, root growth appeared to be favoured to shoot growth. Development of terminal resting buds in most of the seedlings in -P indicated that shoot growth did in fact cease, whereas, roots appeared to grow relatively more than in the -N or Full treatment. Will (1961) suggests that this response to P deficient conditions is due to the ability of the seedling to maintain the level of P in the

root at the expense of the shoot. Little or no lateral branch growth and significantly greater length of roots (LR and TL) produced by seedlings in -NP suggest a similar competition between shoot and root growth. Development of short primary needles and a blue-green tinge to the foliage in some seedlings, both probable symptoms of P deficiency (Will, 1961), further suggest that P may have been translocated to the root.

The final dry weights of shoot and total root, and root: shoot ratio were not significantly different in -N, -P, -NP and Full treatments (Experiments 1 and 2). Relatively little growth in either root or shoot occurred during the rather short treatment period and no significant differences were found. Variation in shoot and root size among seedlings and treatments could easily have masked any real but minor differences in dry weight increments between treatments. High variability in the root growth parameters measured did not appear to be correlated with mycorrhizal root formation, evident in some seedlings. The short branched roots near the top of the root crown were no greater or less in number on seedlings in either treatment. In the three week treatment period these roots rarely showed sufficient growth for their presence to be recorded.

The variation might conceivably be evidence of genetic differences or only be the expression of the number of root tips remaining in good condition following the pruning and trimming procedure. Whatever the reason, this problem of variability in root growth has also been previously observed by Stone (1955), Stone *et al.* (1962) and Abod (1977), in studies using the same technique for assessing the RRP of seedlings.

Results of this experiment emphasized the importance of the careful selection of seedlings to reduce variability in seedling growth. To minimize the variability in future experiments the following steps were taken:

a) growing a large number of seedlings, from which only the most uniform in size were selected.

b) using as many replications as possible within the limitations of the space available and the time required to assess the RRP of seedlings.

Using this method of seedling selection the variability in many parameters measured was reduced. However, variability in root

parameters was still rather high. Such response by morphologically similar seedlings points to the weakness in using morphological criteria in grading seedlings for physiological studies.

A lack of essential nutrients throughout the growth period had marked effects on the shoot and root growth of seedlings prior to and after transplanting into favourable conditions. Seedling growth and development was significantly inhibited by lack of the essential minerals. This is not surprising, as it is well known that deficiencies in the major essential elements impedes growth of trees (Kramer and Kozlowski, 1960; Kozlowski, 1971a). *P. radiata* seedlings, for example, show reduced shoot and root growth when grown under conditions deficient in one major element (Purnell, 1958; Will, 1961) or in all the essential elements (Kanwar, 1959).

Not only is seedling size affected by the nutrient regime but also the seedling nutritional status, as observed by deficiency symptoms (chlorosis, reddening of needles) in the seedlings grown with no nutrients. Together, the initial size and nutritional status of the seedlings account for the differences in root and shoot growth after transplanting. Superior performance in height and root growth of the seedlings grown under the Full nutrient regime could be related to their greater size and better health. The higher root:shoot ratio of seedlings raised with no nutrients could reflect a greater reduction in shoot than root growth in seedlings, a response similar to that of seedlings grown under -NP or -P deficiencies. The difference could also be merely a function of plant size differences due to treatment and not represent any basic shift in root:shoot ratio (Ledig and Perry, 1965).

Although the extreme cases of soil nutritional status, that is, full nutrient and no nutrient, were examined, the results do show that seedling response immediately following outplanting is largely a function of the nutritional status of the seedling which is in turn determined by the nutritional status of the soil in which they were raised. Further evidence of this is shown by the work of Donald (1968), Sanada (1971), Machek (1972/1973) and Woods (1976). These authors all showed that seedlings raised under conditions of nutrient sufficiency performed better once outplanted than those grown under conditions of nutrient deficiency.

For the purposes of the present work, the results of the experiments reported in this chapter are quite clear. If the material used in all of the following experiments was raised and maintained under conditions of adequate nutrient supply then none of the observations on root regeneration made should have been influenced unduly by nutrient factors. All of the experiments involved root-pruning and transplanting of seedlings under conditions of adequate nutrient supply. Only indirectly could nutrient factors be responsible for treatment difference, as for example low temperature conditions restricting the translocation or mobilisation of essential nutrient elements.

CHAPTER 5

THE EFFECTS OF ROOT- AND SHOOT-PRUNING ON THE ROOT REGENERATION POTENTIAL AND SHOOT GROWTH OF *Pinus radiata* SEEDLINGS

5.1 INTRODUCTION

Nursery grown seedlings are usually pruned in various ways before being planted out to the forest. In some species, like *P. radiata* this method of conditioning is sometimes essential for the plants to withstand transplanting. Often, seedlings are root- and/or shoot-pruned in the nursery bed, and/or prior to planting in efforts to improve stock quality (Limstrom, 1963).

The term "root-pruning" has been used indiscriminately in the literature to describe at least two distinct pruning operations (a) before lifting, the severence of roots of seedlings *in situ* in the nursery bed or transplanting line and (b) after lifting and before planting, the clipping of roots of seedlings mainly for convenience in handling and planting. In this chapter, root-pruning will refer to (b) above. "Undercutting", which is also synonymous to the term "root-pruning in place" will be restricted to the operation described in (a). Root "wrenching" is another nursery operation that has often been associated with undercutting in conditioning seedlings (Cameron and Rook, 1969b; Rook, 1971; van Dorsser and Rook, 1972). The term wrenching refers to the process of severing the roots and further disturbing the soil around the roots by partially lifting the seedlings in the soil (Goudie, 1935; Cameron and Rook, 1969b; Rook, 1971; van Dorsser and Rook, 1972).

The objectives of undercutting seedlings in the nursery bed are several:

a) to arrest top growth of seedling stock and encourage diameter growth thus producing a sturdier tree (Stoeckeler and Jones, 1957; Schubert and Adams, 1971; Armson and Sadreika, 1974).

b) to induce the production of a more fibrous root system and improved root:shoot balance (Stoeckeler and Jones, 1957; Sutton, 1969; Schubert and Adams, 1971; Trappe, 1971; Armson and Sadreika, 1974).

c) to facilitate seedling removal from nursery beds (Schubert and Adams, 1971), as pruned seedlings have more root fibre in the upper soil levels they are less likely to lose much fibre at lifting (Faulkner, 1953; Gingerich and Hertel, 1963).

d) to produce seedlings with attributes similar to those of transplants, therefore, a substitute method for transplanting (Stoeckeler and Jones, 1957; Gingerich and Hertel, 1963; Mullin, 1966; Schubert and Adams, 1971; Aldhous, 1972; Armson and Sadreika, 1974).

e) to salvage seedlings, to keep the size of seedlings within bounds if for any reason they must be stood over for a year, otherwise they will grow too big (Cameron and Rook, 1969b; Aldhous, 1972).

Undercutting generally is quite ineffective in reducing top growth of seedlings (Huberman, 1940; Gingerich and Hertel, 1963; Atterson, 1964; Shoulders, 1962; Mullin, 1966; Aldhous, 1972; Ruiter, pers.comm.) and promoting vigorous root development (Faulkner, 1953; Atterson, 1964; Harris *et al.*, 1971a,b; Aldhous, 1972; Williams, 1972; Ruiter, pers.comm.). However, the benefits derived from undercutting in the nursery may vary with the species, time of pruning and the frequency and depth of pruning in relation in root position and soil conditions (Aldrich-Blake, 1930; Wilcox, 1955; Shoulders, 1959b, 1963; Mullin, 1966; Schubert and Adams, 1971; Aldhous, 1972; Armson and Sadreika, 1974).

Results of investigations on the effects of undercutting on field performance of nursery stock are rather inconclusive. Undercutting has been shown to increase survival (Wakeley, 1954; Shipman, 1958; Shoulders, 1959b, 1963; Stoeckeler, 1965; Bell, 1968) or have no effect at all (Mullin, 1957; Atterson, 1964; Shoulders, 1963; Williams, 1972). Species difference, pruning method, time of pruning and planting site conditions may account for these differences.

There are considerable differences in species in respect to their adaptability for transplantation (Goudie, 1935). *P. radiata*, for example, often shows poor survival unless sufficiently wrenched, undercutting may not be enough. Seedlings of *P. radiata* in many parts of Australia and New Zealand make rapid height growth in the late autumn, and, unless this growth is retarded by removal of part of the root, will result in the production of tall, soft plants. Undercutting, followed by repeated wrenching, during the growing season significantly improves the quality of seedling produced. The benefits

of wrenching seedlings in the nursery have been reported by Goudie (1935), van Dorsser (1967, 1969a,b), Cameron (1969), Cameron and Rook (1969a,b), Rook (1969a, 1971), van Dorsser and Moberly (1971), Will *et al.* (1971), van Dorsser and Rook (1972), Benson (1974, 1976a), Bacon (1975), Minko and Craig (1976), Benson and Shepherd (1977) and Chavasse (1977). The importance of conditioning seedlings by wrenching, especially *P. radiata*, is illustrated in these studies by the greater survival percentage and height growth after planting, the increased tolerance to cold storage and the improved resistance to temperature, sun and wind exposure of wrenched seedlings.

Studies on the effects of root-pruning of seedlings on subsequent growth after outplanting have produced varied results, which perhaps indicates that caution needsbe taken in the use of this procedure. Root-pruning has been reported to increase survival (McGee, 1961), reduce survival (Smith and Allen, 1962; Sutton, 1967; Brown, 1969) or have no significant effect on survival (Harris *et al.*, 1971a,b) of seedlings once outplanted. Height growth may also be depressed (McGee, 1961; Smith and Allen, 1962; Larson, 1975) or unaffected (Sutton, 1967; Harris *et al.*, 1971a,b) by root-pruning, whereas, root growth significantly increases (Sutton, 1967; Harris *et al.*, 1971a,b; Kozlowski and Davies, 1975; Larson, 1975). These apparent variations in response to root-pruning could be due to species differences or to local climatic conditions at the field test sites.

Because the balance of physiological processes is affected by removal of roots, root systems severely pruned or stripped of roots during lifting may not be able to function properly immediately after transplanting and consequently the seedlings may die.

The proportion of the root system removed by undercutting, wrenching, root-pruning and lifting appears to have considerable bearing on the growth and/or subsequent field performance of seedlings. The general impression from the literature is that severely reduced root systems by shallow undercutting or wrenching in the nursery or root-pruning before planting reduces survival and/or root and shoot growth (Faulkner, 1953; Mullin, 1957; Limstrom, 1963; Brown, 1969; van Dorsser and Rook, 1972; Larson, 1975). Partial removal of the root system, on the other hand, has less effect on seedling growth and field performance (Adams, 1951; Faulkner, 1953; Wakeley, 1954; Shoulders, 1959b; Sutton, 1967; Bell, 1968; Brown, 1969; Larson, 1975). This is then an indication that severely truncated root systems may be detri-

mental to seedling establishment (Faulkner, 1953; Bilan, 1961; Limstrom, 1963; Hermann, 1964).

Shoot-pruning (referred to in literature as clipping, de-topping, topping, top pruning and shoot decapitation) of seedlings in the nursery bed or at the time of planting also provides a means of modifying seedling size and improving the quality of planting stock (Lanquist, 1966; Stockley, 1975; Rodin and Nikitina, 1976). This practice has been recommended,

a) to supply uniform stock for mechanized planting and facilitate handling of stock (Limstrom, 1963; Larson, 1975).

b) to improve the root:shoot balance of the seedling, under the assumption that higher root:shoot ratios will reduce transpiration and the probability of critical water stress developing in the seedling (Stoeckeler and Jones, 1957; Krinard, 1959; Anon., 1968; Bacon, 1975; Lavender and Hermann, 1976).

c) to stimulate the production of sprouts (Meginnis, 1940).

d) to salvage seedlings which otherwise would be too large if carried over for a further year in the nursery (Stoeckler and Jones, 1957; Lanquist, 1966; Stockley, 1975) or those seedlings that are top-damaged or poorly formed (Meginnis, 1940).

Investigations on shoot-pruning in the nursery bed well before lifting, rather than just prior to planting, have shown favourable results in terms of improved stock quality (Stoeckeler and Jones, 1957; Anon., 1968; Stockley, 1975; Rodin and Nikitina, 1976). Results of work by Rodin and Nikitina (1976) with *Pinus sylvestris* L. indicate shoot-pruning in the nursery produces high quality stock with well formed root systems and optimum root:shoot ratios. Stockley (1975) reports that shoot-pruning in the nursery bed during the active growing season ensures that the wound is calloused by the time of lifting and that the seedlings lifted have sturdy, hardened stocks with strong buds. He also states that in lieu of quality seedling stock, shoot-pruned seedlings are better than large unpruned seedlings, in that they establish well, produce a leader and eventually a sound tree.

Pruning the tops of seedlings at lifting or before planting, however, has not always proven beneficial in improving the field performance of seedlings. Results of investigations are variable, from reduced survival (Meginnis, 1940; Stoeckeler and Jones, 1957; Hermann, 1964; Mullin, 1973; Bacon, 1975) and shoot growth (Meginnis,

1940) in shoot-pruned seedlings to no differences in survival and/or shoot growth between shoot-pruned and unpruned seedlings (Krinard, 1959; Lanquist, 1966; Adams *et al.*, 1967; Bacon, 1975; Minko and Craig, 1976). The planting site conditions, time of pruning, severity of pruning and species involved could account for these differences. Some of the inconsistencies in results of these studies might be accounted for by factors associated with the roots, possibly due to differences in the amount of root lost at the time of lifting.

Shoot-pruning of *P. radiata* seedlings is common practice in both Australian and New Zealand nurseries (Anon., 1968; Shepherd, 1971; Burdon and Bannister, 1973; Bacon, 1975; Stockley, 1975; Minko and Craig, 1976), however, information on the subject is not well documented. Some literature points to the merits and practicality of the technique (Stockley, 1975; Minko and Craig, 1976) whereas, others suggest caution be taken in its application (Bacon, 1975).

P. radiata seedlings appear to have a remarkable ability to withstand severe shoot-pruning although the timing of pruning appears to be important in this regard. Severe pruning of seedlings in the nursery bed well before lifting, however, shows more favourable results in terms of seedling growth or field performance, than pruning the seedlings at lifting or planting. Stockley (1975) reports that *P. radiata* seedlings shoot-pruned from 60 cm down to 10 cm in the nursery well before lifting, produce strong buds and sturdy shoots in time for lifting. In terms of field response, Bacon (1975) found that seedlings pruned to almost half their height, four months before lifting, had superior survival percentages than seedlings pruned at planting. Survival of both intact seedlings and those pruned several months prior to lifting was similar. In another experiment this author found similar results, with poorer survival shown by seedlings shoot-pruned before planting than those unpruned. After two years, the survival and height growth of the seedlings were inversely proportional to the severity of pruning. Results of an investigation by Minko and Craig (1976) also showed that differences in seedling height, the result of different degrees of pruning, persisted after nine months in the transplant bed. Survival of the seedlings was not affected by severity of pruning as shown by Bacon (1975). The nature of the stock, the degree of pruning actually tested and the planting conditions, may easily account for the discrepancy in the results of these trials.

Once again the size and nature of the root systems of the plants involved in these trials need be taken into account. No indication of the state of the root systems at the time of transplanting is given in the studies noted.

The effects of root- and shoot-pruning at planting on the root regeneration potential (RRP) and early growth of *P. radiata* seedlings immediately following planting has not been previously examined. The 4 experiments detailed in this chapter were carried out to investigate these effects. The first experiment examined the effect of root-pruning at planting at different levels of severity on the RRP and shoot growth of seedlings. The second experiment examined the effect of a severe loss of roots on the RRP and shoot growth of seedlings. The third and fourth experiments examined the effect of shoot-pruning at planting at different levels of severity on RRP and shoot growth of seedlings. The effects of root- and shoot-pruning were observed three weeks after planting.

5.2 MATERIALS AND METHODS

P. radiata seedlings (seed origin : Yarralumla, A.C.T.) were grown at either the Forestry Department or CERES phytotron, depending upon where the experiment was performed.

Seedlings used in Experiments 1 and 3 were raised in a Forestry Department glasshouse as described in Chapter 3 (Section 3.3.1). Throughout the growing period the glasshouse temperature was kept above $20^{o}C$ and the day-length was extended to sixteen hours. Seedlings for Experiments 2 and 4 were raised in a CERES glasshouse (facility described in Chapter 3, Section 3.2.1) run at a day/night temperature of $21^{o}/16^{o}C$ with a sixteen hour day-length. Prior to and during the treatment period, all seedlings were watered and fertilized as described in Chapter 3, Section 3.3.3.

In Experiment 1, eighty seedlings of approximately 100-150 mm in height (nearly three months old) were transferred into an LBH cabinet at the Forestry Department (facility described in Chapter 3, Section 3.2.1). The cabinet temperature was set at a day/night temperature of $24^{o}/19^{o}C$ with a sixteen hour day and an eight hour night. Light intensity at plant height was approximately $575\mu Em^{-2}sec^{-1}$ (3000 f.c.). Relative humidity was kept above 40%.

After a three week acclimation period, thirty-two seedlings were carefully selected for the experiment, eight for each treatment. Seedlings were chosen on the basis of uniformity in diameter and height of the shoot and total root mass (determined visually).

In this particular experiment, seedling root systems were not pruned and trimmed for estimation of subsequent root growth as described in Chapter 3 (Section 3.3.4). Rather, all root systems were stained and the only roots removed were those required by the particular pruning treatment. A 1% solution of Safranin O (a red coloured microscopic stain) and water was used to stain the root systems. Preliminary tests showed that growth of seedlings with stained roots was not adversely affected. No symptoms of ill-health were observed.

The staining procedure involved was rather simple. Seedling root systems were submerged into the Safranin O solution for twenty seconds, then drained of excess solution and placed between moist paper towels. After 30-45 seconds, the root systems were carefully rinsed in running water for one minute. After staining, the root systems of the seedlings to be pruned were carefully spread out and roots removed with a scalpel.

The pruning treatments included:-

Control - no roots removed

RP_{25}-25% (approximately) of the total root mass removed

RP_{50}-50% (approximately) of the total root mass removed

RP_{75}-75% (approximately) of the total root mass removed.

The amount of root removed was determined visually for each root system. All roots removed were kept for dry weight estimations. After pruning the seedlings were repotted into moist perlite and vermiculite and returned to the growth cabinet. Pot location in the cabinet was completely randomized.

After three weeks, the seedlings were harvested. Root regeneration potential, diameter and height increment, final dry weights of shoot, regenerated root and total root, dry weight of root removed, and root:shoot ratio were determined as described in Chapter 3, Section 3.4. Root regeneration potential was based on the number of new roots 0.5-1.4 cm (SR), $\geq$ 1.5 cm (LR) and $\geq$ 0.5 cm (GT), and the length of LR (TL) produced by each seedling. The moisture content of the shoot of each seedling was also determined, using the formula,

$$MC_S = \frac{FW-DW}{DW} \times 100$$

where, MC_S = moisture content of the shoot in per cent.

FW = fresh weight of the shoot in grams.

DW = dry weight of the shoot in grams.

Shoots were severed 10 cm below the cotyledons. The fresh weights were measured immediately after the seedlings were removed from the cabinet. Dry weights were determined as described in Chapter 3 (Section 3.4).

In Experiment 2, two lots of *P. radiata* seedlings were used. Seedlings in Lot 1 were 127 days old, and smaller in diameter and height than the seedlings in Lot 2 which were 197 days old (see Table 5.2). All seedlings were raised at 21°/16°C day/night temperature in a glasshouse at the CERES phytotron up until the time of treatment.

Eight seedlings of uniform size from Lot 1 and four seedlings from Lot 2 were chosen for each treatment. All seedling root systems were carefully removed from the pots and thoroughly washed before treatment. The treatments included: T_1-pruning the root system to 9 cm from the cotyledons, removing (with scalpel) all the fine rootlets from the primary (tap) and secondary (main lateral) roots and removing any white root tips remaining on the root system. T_2-pruning the root system to 9 cm from the cotyledons and removing only the new white root tips on the root system. All roots removed were kept for dry weight estimations.

After pruning, seedlings were repotted and staked. Staking was essential for seedlings in T_1, especially from Lot 2, as the root systems remaining after pruning were not sufficient to hold the plants securely in the pots in an upright position. Seedlings were returned to the glasshouse. Pot location on the glasshouse bench was completely randomized. Special care was taken to ensure that larger trees did not shade the smaller ones.

Three weeks after treatment, all seedlings were harvested. Root regeneration potential, diameter and height increment, relative growth rate of diameter (RGR_D) and height (RGR_H), final dry weights of shoot and total root, dry weight of root removed and root:shoot ratio were determined for each seedling. New roots produced by seedlings especially from Lot 1 weren't very long,therefore, a much shorter root length was used to designate long (LR) and short (SR) roots. Root regeneration per seedling, including the number of new

white roots 0.1-0.5 cm (SR), 0.6-1.4 cm (MR) ≥ 1.5 cm (LR), and ≥ 0.1 cm (GT).

In Experiment 3, fifty 4 month old seedlings raised in a Forestry Department glasshouse were transferred into an LBH cabinet. The cabinet was set at the same day/night temperature ($24^{o}/19^{o}C$), photoperiod (sixteen hours), light intensity ($575\mu Em^{-2}sec^{-1}$) and relative humidity (40%) as in Experiment 1. Seedlings were acclimatised to this environment for two and a half months prior to root-pruning.

Twenty seedlings of uniform size were selected for treatment. The root system of each seedling was thoroughly washed, pruned to 21 cm from the cotyledons and any white root tips remaining were pinched off. Once root-pruned and -trimmed the seedlings were repotted and staked. Ten of the seedlings were used as a control (Control), in which no shoots were removed. The shoots of the other ten seedlings were severed with a sharp scalpel 5 cm from the apex or approximately 23% of the shoot by length (SP_{23}). Petroleum jelly was used to cover the cut surface to reduce stem water loss and check possible attack by pathogens. After shoot-pruning, the seedlings were returned to the growth cabinet for another three weeks until the harvest. Pot location in the cabinet was completely randomized.

At harvest, the root regeneration potential, diameter increment, final dry weights of shoot, newly regenerated root and total root, dry weight of shoot removed, and root:shoot ratio were determined for each seedling. Root regeneration potential was based on the number of new white roots 0.5-1.4 cm (SR), ≥ 1.5 cm (LR), ≥ 0.5 cm (GT), and the total length of LR (TL) produced by each seedling.

Experiment 4 was conducted in a CERES phytotron glasshouse. Seedlings used in the experiment were raised in a glasshouse run at $21^{o}/16^{o}C$ as described earlier in this section. Five weeks prior to treatment, forty seedlings were transferred to a glasshouse run at a day/night temperature of $24^{o}/19^{o}C$.

After the acclimation period, sixteen seedlings of uniform size were chosen for treatment. The root system of each seedling was pruned to 21 cm from the cotyledons and all the white root tips

remaining were pinched off. Once repotted, seedlings were staked and shoot-pruned. The treatments included, SP_{12}, 12% of the total shoot length removed and SP_{36}, 36% of the total shoot length removed. All shoots were severed with a sharp scalpel and the cut surface covered with petroleum jelly. Seedlings were returned to the glasshouse ($24^{o}/19^{o}C$) for another three weeks, after which time the seedlings were harvested.

The data collected at the harvest was the same as in Experiment 3.

5.3 STATISTICAL ANALYSIS

In Experiment 1, differences between treatment means of each parameter were compared using Duncan's multiple range test at the 5% level of significance.

Comparisons of treatment means for each parameter measured in Experiment 2,3 and 4 were made by t-test. In Experiment 2, only the differences between treatment means within each Lot were tested for significance. Differences in treatment means between Lot 1 and Lot 2 were not compared.

Coefficients of variability were calculated for each parameter in all experiments. Results of the analyses of Experiments 1 and 2 are presented in Tables 5.1 and 5.2 respectively. Results of Experiments 3 and 4 are presented together in Table 5.3.

5.4 RESULTS

5.4.1 Experiment 1

5.4.1.1 Root Regeneration Potential

The results of the analysis (Table 5.1) show that all pruning treatments regardless of severity, significantly reduced the root regeneration potential (RRP) of the seedlings. Differences between the pruning treatments RP_{25}, RP_{50} and RP_{75}, for all root parameters were not significant.

Seedlings in the Control, with no roots removed, produced significantly greater numbers of new white roots 0.5-1.4 cm (SR), $\geq$1.5 cm (LR) and $\geq$0.5 cm (GT) and greater total length of LR (TL) than produced by seedlings in the pruning treatments RP_{25}, RP_{50} and RP_{75}.

Table 5.1 Effects of root-pruning on the RRP and shoot growth of *P. radiata* seedlings measured 3 weeks after planting (Experiment 1), where 75%, 50% or 25% of the root was removed (RP_{75}, RP_{50}, RP_{25}).

Parameter	Treatment Mean [1] (C.V.)[2]			
Root Regeneration				
Number of new roots ≥0.5 cm (GT)	27(44.9) RP_{75}	32(60.3) RP_{50}	36(20.9) RP_{25}	70(35.6) C
Number of new roots ≥1.5 cm (LR)	8(41.7) RP_{75}	17(57.7) RP_{50}	19(34.1) RP_{25}	36(41.5) C
Number of new roots 0.5-1.4 cm (SR)	15(65.4) RP_{50}	16(41.0) RP_{25}	18(49.0) RP_{75}	34(54.4) C
Length of new roots ≥1.5 cm (TL) in cm	21.6(48.7) RP_{75}	50.8(64.4) RP_{50}	58.8(49.2) RP_{25}	133.9(52.2) C
Height and Diameter				
Initial diameter (mm)	4.02(8.1) C	4.12(9.4) RP_{75}	4.14(4.8) RP_{50}	4.16(6.4) RP_{25}
Diameter increment (mm)	0.30(47.9) RP_{75}	0.37(57.4) RP_{50}	0.56(40.6) RP_{25}	0.90(26.2) C
Initial height (cm)	11.98(19.0) C	13.06(9.2) RP_{75}	13.76(22.2) RP_{50}	13.86(10.6) RP_{25}
Height increment (cm)	0.75(54.7) RP_{75}	1.30(46.9) RP_{50}	1.62(31.5) RP_{25}	1.99(30.0) C
Moisture Content				
Shoot (%)	191.0(11.3) RP_{75}	205.0(4.2) RP_{50}	224.0(4.4) RP_{25}	231.0(8.9) C
Final Dry Weight				
Shoot (g)	4.884(18.3) RP_{50}	4.936(9.7) RP_{75}	5.690(18.6) RP_{25}	5.868(22.5) C
Regenerated root (g)	0.052(44.3) RP_{75}	0.086(44.3) RP_{25}	0.099(77.7) RP_{50}	0.160(48.3) C

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Table 5.1 (Cont'd)

Parameter	Treatment Means[1] (C.V.)[2]			
Total root (g)	0.916(17.6) RP_{75}	1.270(23.3) RP_{50}	1.696(14.8) RP_{25}	2.342(12.1) C
Root removed (g)	0.000(0.0) C	0.244(21.5) RP_{25}	0.534(29.5) RP_{50}	0.682(28.0) RP_{75}
Root:shoot ratio	0.19(10.5) P_{75}	0.26(6.9) P_{50}	0.30(8.5) P_{25}	0.41(13.4) C

1 Mean of 8 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

The total number of new roots (GT), for example, produced by seedlings in the pruning treatments was almost half the number produced by Control seedlings.

Removal of up to 50% of the roots, markedly reduced LR and consequently the total length of LR. Removal of 75% of the roots resulted in a much greater reduction in LR and TL, but the differences between RP_{25}, RP_{50} and RP_{75} were not significant.

5.4.1.2 Diameter and Height

Diameter and height increment were significantly affected by removal of the roots. Seedlings in the pruning treatments RP_{25}, RP_{50} and RP_{75} all grew less in diameter than the Control seedlings. There were no significant decreases in diameter growth in seedlings between treatments RP_{25} and RP_{50}, or between treatments RP_{50} and RP_{75}, however, removing 25% of the roots (RP_{25}) resulted in significantly better diameter growth in seedlings than did removing 75% of the roots. In treatment RP_{25} diameter increment was almost twice that of treatment RP_{75}.

Height growth was not as sensitive to root removal as was diameter growth. Height increment of seedlings with 25% of the roots removed was not significantly different from seedlings with no roots removed. Seedlings in the control grew more in height than the seedlings with more than 25% of their roots removed and seedlings in the least severe pruning treatment, RP_{25} grew more in height than those in the most severe treatment , RP_{75}.

5.4.1.3 Moisture Content of the Shoot

The moisture content of the shoot (% MC_s) of seedlings in the Control and pruning treatments RP_{25} and RP_{50} were not significantly different. Removal of 50% of the root resulted in a much lower % MC_s than in the Control. Severe root pruning, RP_{75}, reduced % MC_s further although the difference between treatments RP_{75} and RP_{50} was not significant.

5.4.1.4 Final Dry Weight

Significant differences in the weight of root removed and the final total root weight between treatments were not unexpected

(see Table 5.1). The weight of root removed increased with the proportion of the root mass pruned, while final total root weight increased with decreasing severity of pruning.

Differences in the dry weights of regenerated root between treatments RP_{25}, RP_{50}, RP_{75} and the Control were significant, reflecting the better root growth response in the Control compared to that of the other treatments. No significant differences were found in the final shoot dry weight between treatments. Root:shoot ratios of seedlings in treatment RP_{75} and the Control were significantly different from the other treatments. Root:shoot ratios of seedlings in treatments RP_{50} and RP_{25} were similar.

5.4.2 Experiment 2

5.4.2.1 Root Regeneration Potential

Removal of the fine rootlets from root systems (T_1) significantly reduced the number of new white roots 0.1-0.5 cm (SR), 0.6-1.4 cm (MR), and the total number of new white roots (GT) produced by both small (Lot 1) and large (Lot 2) seedlings. Table 5.2 shows that the large seedlings produced more roots (SR, MR, GT) in treatment T_2 with no fine roots removed than the small seedlings. These differences in root parameters between Lot 1 and Lot 2 seedlings were not tested, however, differences between treatments within Lot 1 and Lot 2 were found to be significant. In treatment T_2, for example, the large seedlings produced 316 new white roots (GT) and the small seedlings produced 22, each significantly higher than 0 and 1 root produced in T_1 by large and small seedlings respectively. Another difference in root growth between large and small seedlings in the two treatments was the number of new white roots $\geq$ 1.5 cm (LR) produced. The large seedlings produced 62 LR in treatment T_2, whereas, the small seedlings did not produce any.

As shown in Table 5.2, new root growth, as defined by the parameters in the experiment for both Lot 1 and Lot 2 seedlings in treatment T_1 was practically nil. Each seedling in T_1 did, however, develop 100 or more small white nodules along the remaining primary and lateral roots. These nodules appeared to be the early stages of development of new 'initiated' roots. Very few nodules, as described above,were produced on seedling root systems in T_2.

Table 5.2 Effects of the removal of fine rootlets on shoot and root growth of small (Lot 1) and large (Lot 2) *P. radiata* seedlings measured 3 weeks after planting (Experiment 2). T1, roots pruned to 9cm, all fine rootlets removed; T2, roots pruned to 9cm.

Parameter	Lot 1				Lot 2			
	treatment	mean[1]	C.V.[2]		treatment	mean[1]	C.V.[2]	
Root Regeneration								
Number of new roots 0.1-0.5 cm (SR)	T1	1	>100.0		T1	0	00.0	
	T2	17	79.9	**	T2	115	20.7	***
Number of new roots 0.6-1.4 cm (MR)	T1	0	00.0		T1	0	00.0	
	T2	5	57.6	***	T2	138	5.9	***
Number of new roots ≥1.5 cm (LR)	T1	0	00.0		T1	0	00.0	
	T2	0	00.0	NS	T2	62	17.3	***
Number of new roots ≥0.1 cm (GT)	T1	1	>100.0		T1	0	0.0	
	T2	22	60.7	***	T2	316	8.2	***
Diameter and Height								
Initial diameter (mm)	T1	2.78	9.3		T1	7.05	11.3	
	T2	2.94	11.0	NS	T2	7.40	11.2	NS
Diameter increment (mm)	T1	0.04	65.9		T1	0.07	41.4	
	T2	0.16	39.4	***	T2	0.22	61.8	NS
Initial height (cm)	T1	15.06	13.7		T1	45.32	10.8	
	T2	15.92	17.7	NS	T2	46.72	11.0	NS
Height increment (cm)	T1	0.59	80.5		T1	0.62	63.2	
	T2	1.02	40.3	NS	T2	3.20	13.2	***
Final Dry Weight								
Shoot (g)	T1	1.506	16.39		T1	16.922	31.2	
	T2	1.669	17.19	NS	T2	22.462	32.4	NS
Total root (g)	T1	0.292	19.48		T1	1.845	20.7	
	T2	0.436	11.92	***	T2	2.915	4.5	***
Root:shoot ratio	T1	0.19	7.20		T1	0.11	7.12	
	T2	0.26	5.06	***	T2	0.14	14.83	NS

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Table 5.2 (Cont'd)

Parameter	Lot 1				Lot 2			
	treatment	mean[1]	C.V.[2]		treatment	mean[1]	C.V.[2]	
Root removed (g)	T1	0.270	21.11		T1	3.896	8.8	
	T2	0.169	21.84	***	T2	2.472	20.1	***

1 Mean of 8 replicates (Lot 1), 4 replicates (Lot 2).

2 C.V. = Coefficient of Variability in per cent.

Note: Significance levels: * P<0.05, ** P<0.01, *** P<0.001, NS non significant.

Although not presented in Table 5.2, three small seedlings in treatment T_1, each produced 2 new white roots, 0.1-0.5 cm long. Each new root was produced on a fine rootlet that had been left behind at the time of pruning. Of all the seedlings in T_1, only these three showed evidence of succulent new shoot growth after three weeks.

5.4.2.2 Diameter and Height

The height and diameter response to treatments T_1 and T_2 were different for small and large seedlings. Diameter increment in the smaller seedlings was significantly reduced by the removal of the fine roots. Seedlings in treatment T_1 produced four times less diameter than those seedlings in T_2. Height increment, on the hand was not significantly affected by severe root removal in T_1.

The large seedlings responded in quite the opposite way. Height increment, rather than diameter increment was significantly reduced by the removal of fine roots. Height increment of seedlings in treatment T_2 was almost five times that of seedlings in treatment T_1, with only a 0.62 cm height increase in T_1 and a 3.20 cm height increase in T_2. Diameter growth of large seedlings was not significantly affected by severe root removal.

5.4.2.3 Final Dry Weight

Differences in the final total root dry weight and the weight of root removed between treatments were significant for both small and large trees. The weight of root removed was highest in treatment T_1 where the largest amount of root was removed and the highest final total root dry weight was in treatment T_2, where the least amount of root was removed.

Removal of few roots from seedlings in treatment T_2 resulted in higher root:shoot ratios in T_2 than in T_1, however, these differences were significant only in the small seedlings.

5.4.3 Experiments 3 and 4

5.4.3.1 Root Regeneration Potential

Table 5.3 shows that in Experiment 3, shoot-pruning had a marked effect on the RRP of the seedlings. The number of new white roots 0.5-1.4 cm (SR), $\geq$ 1.5 cm (LR) and $\geq$ 0.5 cm (GT), and the total

Table 5.3 Effects of shoot-pruning on RRP and shoot growth of *P. radiata* seedlings measured 3 weeks after planting (Experiment 3 and 4). Treatments SP_{12}, SP_{23}, SP_{36} represent 12%, 23% and 36% of the shoot removed respectively.

Parameters	Experiment 3				Experiment 4			
	treatment	mean[1]	C.V.[2]		treatment	mean[1]	C.V.[2]	
Root Regeneration								
Number of new roots ≥0.5 cm (GT)	C	291	45.6		SP_{12}	113	38.2	
	SP_{23}	121	87.4	***	SP_{36}	34	>100.0	***
Number of new roots ≥1.5 cm (LR)	C	107	21.3		SP_{12}	48	62.0	
	SP_{23}	32	83.5	***	SP_{36}	13	>100.0	**
Number of new roots 0.5-1.4 cm (SR)	C	184	68.8		SP_{12}	65	30.3	
	SP_{23}	89	95.5	*	SP_{36}	21	95.8	**
Length of new roots ≥1.5 cm (TL) in cm	C	328.9	28.3		SP_{12}	160.3	87.1	
	SP_{23}	83.2	79.1	***	SP_{36}	30.7	>100.0	*
Diameter and Height								
Initial diameter (mm)	C	5.94	11.4		SP_{12}	6.34	12.3	
	SP_{23}	6.12	8.2	NS	SP_{36}	6.31	11.4	NS
Diameter increment (mm)	C	0.66	41.7		SP_{12}	0.35	27.7	
	SP_{23}	0.29	63.9	***	SP_{36}	0.16	68.5	***
Initial height (cm)	C	21.16	18.0		SP_{12}	40.54	19.2	
	SP_{23}	21.90	9.5	NS	SP_{36}	43.28	21.8	NS
Final Dry Weight								
Shoot (g)	C	12.958	24.5		SP_{12}	13.240	24.6	
	SP_{23}	9.633	21.4	***	SP_{36}	10.914	27.2	***
Regenerated root (g)	C	0.341	37.2		SP_{12}	0.227	>100.0	
	SP_{23}	0.083	74.2	***	SP_{36}	0.032	95.6	*
Total root (g)	C	3.154	14.6		SP_{12}	3.420	18.9	
	SP_{23}	2.483	17.7	***	SP_{36}	3.380	20.0	NS

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Table 5.3 (Cont'd)

Parameters	Experiment 3				Experiment 4			
	treatment	mean[1]	C.V.[2]		treatment	mean[1]	C.V.[2]	
Shoot removed (g)	C	0.000	00.0		SP_{12}	0.745	35.4	
	SP_{23}	1.450	41.8	***	SP_{36}	2.212	26.9	***
Root:shoot ratio	C	0.25	12.4		SP_{12}	0.27	13.3	
	SP_{23}	0.26	8.8	NS	SP_{36}	0.32	9.0	NS

1 Mean of 10 replicates (Experiment 3), 8 replicates (Experiment 4).

2 C.V. = Coefficient of Variability in per cent.

Note: Significance levels: * $P<0.05$, ** $P<0.01$, *** $P<0.001$, NS non significant.

length of LR (TL) produced by seedlings was reduced by removal of part of the shoot. Similar reductions in root growth were found in Experiment 4, when severity of pruning was increased.

In Experiment 3, for example, removing 23% of the shoot (SP_{23}) reduced the total number of new roots (GT) produced to less than half that produced in the Control. An average of only 121 new roots was produced by seedlings in SP_{23} compared to 291 new roots produced by seedlings in the Control. Of all the root parameters measured, shoot removal resulted in a marked decrease in the numbers and total length of LR produced by seedlings. Seedlings in the Control produced 4 times the number and length of LR than produced in SP_{23}.

In Experiment 4, RRP markedly decreased with an increase in the severity of shoot-pruning. The total number of new roots (GT) and the total length of LR (TL) produced by seedlings in SP_{36} were almost four times less than that produced by seedlings in SP_{12}. However, even with 36% of the shoot removed a total number of 34 new roots were produced by seedlings.

5.4.3.2 Diameter

Shoot-pruning greatly affected diameter growth of the seedlings. The differences in diameter increment between treatments in both Experiments 3 and 4 were significant. As shown in Table 5.3, diameter growth was significantly reduced by removal of part of the shoot in Experiment 3, and by the increased severity of shoot-pruning in Experiment 4.

5.4.3.3 Final Dry Weight

Differences in the final dry weights of the shoot, regenerated root and the shoot removed between treatments in both Experiments 3 and 4 were significant.

In Experiment 3, the final dry weights of the total root were significantly greater in the control than the pruning treatment, SP_{23}. The lower weight of new regenerated roots in SP_{23} than in the Control could account for the difference. In Experiment 4, the final dry weight of the total root was not significantly different between treatments, even though regenerated root weights were significantly different. Root:shoot ratios between treatments in both experiments

were similar, despite the removal of rather large portions of the shoot.

5.5 SUMMARY OF RESULTS

5.5.1 Experiment 1

(i) All pruning treatments, RP_{25}, RP_{50} and RP_{75} significantly reduced the numbers (SR, LR, GT) and length (TL) of new roots produced by seedlings. Differences in these parameters between pruning treatments were not significant. Seedlings in the Control showed superior growth in all root parameters.

(ii) Removal of roots, regardless of severity reduced diameter and height growth in seedlings. Seedlings in treatment RP_{75}, all grew less than the Control seedlings. Height growth of seedlings in RP_{25}, although less was not different to the Control.

(iii) Removal of 50% or 75% of the root reduced the % MC_s of seedlings. Severely pruned seedlings, i.e., RP_{75}, had significantly lower % MC_s than seedlings with 25% or no root removed.

(iv) Differences in final total root weight and weight of root removed between treatments were significant and corresponded with the severity of the root-pruning treatment. The greater root growth of seedlings (SR, LR, GT, TL) in the Control is reflected in the greater weight of regenerated roots in the Control, compared to treatments RP_{25}, RP_{50} and RP_{75}.

(v) Seedlings in RP_{75} had lower root:shoot ratios than in the Control and treatments RP_{50} and RP_{25}. The differences in the root:shoot ratio between seedlings in the Control and all pruning treatments were significant. Root:shoot ratios in RP_{50} and RP_{25} were similar.

5.5.2 Experiment 2

(i) The numbers of roots (SR, MR, GT) produced by both Lot 1 (small) and Lot 2 (large) seedlings were markedly reduced by removal of fine rootlets from the root system.

(ii) Large seedlings produced greater numbers of roots (SR, MR, GT) and longer (LR) roots in treatment T_2 than the small seedlings, but the differences between seedling sizes were not tested.

(iii) Seedlings in T_1, regardless of size, produced many small white nodules along the primary and lateral roots. These nodules were new initiated root.

(iv) Diameter growth in small seedlings was more sensitive to removal of fine roots than was height growth. Diameter increment of seedlings was significantly higher in treatment T_2 than in T_1, whereas differences in height increment between treatments were not.

(v) The large seedlings showed greater response to treatment in height growth rather than diameter growth. Height increment was significantly reduced in treatment T_1 but diameter increment was not different between treatments.

(vi) The significant differences in final dry weight of total root and weight of root removed between treatments for both small and large seedlings corresponded to the severity of the pruning treatment.

(vii) Final shoot weights of the small and large seedlings were not different between treatments. Root:shoot ratios of the small seedlings were greater in treatment T_2 than T_1. Similar differences were not shown in larger seedlings.

(viii) Three small seedlings in treatment T_1 produced 2 new roots, on fine rootlets left behind at pruning. Each seedling showed evidence of succulent new shoot growth.

5.5.3 Experiments 3 and 4

(i) Removal of a portion of the shoot (Experiment 3) significantly reduced the numbers (SR, LR, GT) and the length (TL) of new roots produced.

(ii) Reductions in root growth occurred between treatments in Experiment 4, where 12% and 36% of the shoot (by length) were pruned. Root growth was significantly reduced by severity of pruning.

(iii) Diameter growth in seedlings was sensitive to removal of part of the shoot (Experiment 3) and to a greater proportion of shoot removed (Experiment 4). In Experiment 3, diameter increment in the Control seedlings was greater than in treatment SP_{23}, and in Experiment 4 greater in SP_{12} than SP_{36}.

(iv) Differences in the final dry weights of the shoot, shoot removed and regenerated root between treatments in both Experiments 3 and 4 were significant and corresponded to the differences in the amount of shoot removed and the numbers and length of new roots produced.

(v) The differences in total root weight of seedlings between treatments were not significant in Experiment 4 but were in Experiment 3.

5.6 DISCUSSION

The following conclusions can be drawn from the four experiments examined:

(a) root- and shoot-pruning at planting may be a hazardous practice, as shoot and root growth is reduced immediately following planting at a time critical to plant survival.

(b) growth responses of root- and/or shoot-pruned seedlings immediately following planting is related to the severity of the pruning treatment.

(c) preservation of the fine rootlets on the root systems of seedlings is essential for the immediate subsequent growth of seedlings once outplanted.

The most striking result of these experiments was that root- and shoot-pruning caused a severe and immediate reduction in the growth of seedlings. It is apparent from the results that the amount of root or shoot removed determines the extent to which seedling growth is depressed after planting. The reduced diameter and height growth of seedlings due to root-pruning is followed by the rapid proliferation of new roots or at least evidence of the initiation of new root regardless of the severity of the pruning treatment. Shoot development does not, however, show the same rapid regeneration as is evident for root development.

The immediate depression in shoot growth and the proliferation of new roots, even on a markedly reduced root system indicates a change in the pattern of seedling growth, that priorities are given to the development of new roots. Similar changes in seedling growth patterns occur in seedlings transplanted, undercut and/or wrenched in the nursery (Atterson, 1964; van Dorsser, 1969b; Rook, 1969a,b, 1971; Will *et al.*, 1971; Aldhous, 1972; van Dorsser and Rook, 1972; Benson, 1974; Minko and Craig, 1976), in seedlings planted directly to the forest (Rook and Hobbs, 1972) and in plants deliberately root-pruned in experiments (Humphries, 1958, 1960; Maggs, 1964, 1965; Macpherson, 1970).

Regardless of the severity of root- and shoot-pruning in the treatments examined, all seedlings were able to overcome the initial transplanting shock and were capable of sustaining life. The experimental conditions were more favourable to the plants than many field situations. Seedlings in Experiment 2, with all the fine rootlets removed would be representative of much of the stock lifted and planted

in Australia, which has had no nursery history of undercutting and/or wrenching. The seedlings show a remarkable ability to survive and yet at the same time to engage in the proliferation of many new root apices, thus making provision for subsequent growth. It is surprising that seedlings can even survive with such reduced root systems when compared to seedlings that have been previously conditioned by undercutting and/or wrenching or seedlings with less severely damaged root systems.

Active root tips constitute a major portion of the absorption surface of the root system in nursery seedlings. When seedlings are undercut and/or wrenched or lifted from the nursery some damage to this active system of root tips must occur. In instances where seedlings are severely stripped of finer roots, the remaining portions of suberized primary and lateral roots must be the only absorbing surfaces available to the seedlings. The seedlings are able to obtain water and nutrients through these suberized roots (Crider, 1933; Addoms, 1946; Kramer, 1946; Kramer and Bullock, 1966; Chung and Kramer, 1975), and under favourable conditions maintain the internal water balance of the seedlings above the critical level until new roots develop. However, it is inevitable that internal water deficits will follow if the root surface is inadequate to supply the water lost by the transpiring shoots (see Cameron and Rook, 1969b; Rook, 1973 ; Kozlowski and Davies, 1975).

The reduced moisture content of the shoots of seedlings with severely pruned roots (Experiment 1) indicates that seedlings did undergo some water stress. Further evidence of the development of water stress in seedlings was shown by the desiccation of primary needles and of secondary needle tips in all treatments, as described in Chapter 4 (section 4.4.1.3). Needle desiccation was evident two days after planting, which indicated that water loss occurred immediately after the seedlings were planted. Presumably by altering the root:shoot ratios a greater amount of moisture was lost through transpiration than could be absorbed by the pruned root system. The seedlings did not wilt, nor did the terminal apices of the main leader or branches die under the favourable moisture and temperature regimes of the experiments. Under field conditions these seedlings would inevitably suffer a more severe moisture loss than actually observed.

In the nursery, especially under dry conditions, it is a common occurrence for seedlings to wilt after being undercut and/or wrenched (e.g. Benson, 1974). This drastic loss in turgidity is only temporary and the seedlings, provided with favourable conditions, recover from the initial shock. In the field the wilted leaders of these seedlings often do not recover, so that either the tip of the shoot or the total shoot dies (Adams *et al.*, 1967; Benson, 1974, 1976a; Minko, 1974; Benson and Shepherd, 1977). There is a basic difference between the root systems in each of these two situations, which on the basis of the present results will be critical for seedling survival. In the nursery, many fine roots remain intact after undercutting and/or wrenching, and in many instances must still retain intimate contact with the soil particles and soil moisture reserves. Thus, these plants are able to recover turgidity rapidly. The root systems of lifted seedlings will possess few fine roots, only the larger laterals remain intact, and so will require a much longer time to regenerate new roots and to re-establish contact with both nutrient and water reserves in the soil. Gürth (1970), Lüpke (1973) and Havranek (1975), as described by Lavender and Hermann (1976), conclude from recent investigations with *Picea abies* that the damage incurred to the root systems prior to planting greatly impairs the uptake of water by seedlings after planting. Until the seedling establishes more intimate contact with the soil, the existing roots would not be able to maintain the seedling successfully.

Investigations by Rook (1969a,b), Benson and Shepherd (1977) and van Dorsser (1969b) with wrenched and unwrenched seedlings have indicated that water stress of seedlings after planting in the forest is largely determined by the preconditioning history of the plants or the quality of the seedlings in terms of an efficient root system and hardened shoot. Seedlings with no previous preconditioning by undercutting and wrenching have soft, green and actively growing shoots. The root systems are often severely damaged. Such plants become severely wilted under dry conditions after planting, fail to recover full turgor and die. Previously wrenched seedlings are able to maintain adequate turgor under similar conditions. The hardened stems, i.e. dry, lignified, browned, and greater root surface area of wrenched seedlings reflects a shoot capable of withstanding greater environmental stresses and an efficient root system for absorbing water and nutrients, for maintaining high plant internal water contents and for supporting higher rates of seedling transpiration.

The newly planted seedlings, especially those with only the basic framework of a root system remaining after lifting, must depend to a large extent on food reserves accumulated before planting for subsequent growth (Kozlowski and Keller, 1966; Krueger, 1967a; Ronco, 1973). Investigations into the effects of undercutting and/or wrenching on seedling growth have shown that changes do occur in the translocation of current photosynthates (Rook, 1971; van Dorsser and Rook, 1972) and foliar nutrients (Ruiter, pers.comm.; For. Timb. Bur., 1971b; Benson, 1976a) in seedlings after severing the roots. Current photosynthates and foliar nutrients are channelled from the shoot to the roots to allow seedlings to develop new roots to establish quickly. The direct alteration of the photosynthetic surface, nutrient and food reserves by shoot-pruning no doubt, results in a disturbance in the internal growing conditions of the seedling and this could in turn affect the photosynthetic mechanism of the seedling (Sweet and Wareing, 1966; Wood, 1969). To what extent the seedlings actually depend on the mobilizing of stored food and nutrient reserves is not known. It would appear that a seedling with a better developed root system may rely on these reserves for a much shorter period than would seedlings with a poor root system, or a root system which has been cut off or mutilated at transplanting.

From the results of these experiments it is apparent that when seedlings are undercut and/or wrenched in the nursery, or lifted and planted to the forest, there is a definite setback in seedling growth, followed by a change in the physiological and metabolic activity of the seedling which favour the proliferation of new roots. Consequently, further studies as described in later chapters of this thesis, were undertaken to determine any changes in stomatal resistance, rates of photosynthesis and dark respiration, and the translocation of photosynthates in seedlings, in attempts to explain the change in seedling growth pattern after root removal.

A hormonal imbalance could account for these patterns of growth following the removal of part of the root or shoot. The important role of the roots, especially the root tips, and the shoot in the overall hormonal physiology and growth of plants is well known (Burström, 1953; Åberg, 1957; Street, 1966; Kozlowski, 1971a; Torrey, 1976) and it is inevitable that an imbalance would occur especially if a large portion of either the shoot or root were removed. Previous investigations have demonstrated that certain growth substances are exported

from the shoot to the root and that they have some function there (Burström, 1953; Street, 1966; Zaerr, 1967; Lavender and Herman, 1970; Torrey, 1976). Studies with *P. ponderosa*, however, have indicated that of these growth substances, indoleacetic acid, vitamin B (Fowells, 1943) and auxin (Zaerr, 1967) appear to be relatively ineffective in promoting root initiation.

Sweet and Rook (1972) found that removing the root tips of *P. radiata* by undercutting and wrenching reduces the inhibitor levels in the root and that this reduced inhibitor level is associated with a greatly increased relative growth rate of the roots. Very recent investigations by G.J. Bacon, Forestry Department, A.N.U. on wrenched *Pinus caribaea* reveal contrasting results. Bacon found that the water stress which seedlings experience immediately after being wrenched induces increased levels of abscisic acid, together with reductions in both cytokinin and gibberellin levels. While there exists contradictory evidence as to exactly what hormonal changes occur when roots are removed, the presence of active roots and hence active points of meristematic activity as shown in Experiment 2, may be necessary for the initiation of new shoot growth.

P. radiata seedlings given favourable planting conditions have a remarkable ability to survive drastic alterations of their root systems and successfully divert their resources into the proliferation of new roots. It is obvious from the results of these experiments that seedlings lifted and planted to the forest without any previous history of conditioning in the nursery have reduced chances of survival. When lifted from the nursery and planted these seedlings are not only characterized by greatly reduced root systems with virtually no roots remaining for immediate elongation or initiation of new roots, but, a shoot too soft to withstand the initial shock of being transplanted. Desiccation of the terminal apex of the shoot of severely shocked seedlings can result in leader death which, in turn will slow down the early establishment and rapid growth of the seedlings, which can be characteristic of *P. radiata* under favourable conditions. Wright (1969) found that the death of the leader immediately after planting can render seedlings susceptible to fungal infection which can further reduce growth.

Seedlings sufficiently conditioned in the nursery with a well-developed fibrous root system and hardened shoot could better withstand any harsh environmental conditions at or after planting including drought and higher temperatures, and immediately respond to the new environment. Root systems of conditioned seedlings make better contact with the soil once planted and because of a more fibrous root system have a greater potential for regenerating roots (Cameron and Rook, 1969b; Rook, 1969b).

P. radiata seedlings are generally transplanted to the field under the cooler climatic conditions of winter. Seedlings with a better developed root system and a hardened shoot are able to achieve immediate contact with the new soil environment, to maintain themselves much longer under prevailing drought, and therefore, have a much greater opportunity for rapid recovery and getaway when better climatic conditions prevail than seedlings which are not conditioned.

Regardless of whether seedlings are preconditioned or not, any factor which inhibits the proliferation of new roots immediately after planting jeopardizes possible survival and early growth of these seedlings. The environmental conditions of the planting site or in the case of undercutting and/or wrenching, the environment of the nursery appear largely to determine the ability of the seedling to take advantage of any soil moisture and nutrient reserves, and to become self-supporting by producing sufficient assimilate for new growth (van Dorsser and Rook, 1972). The extent to which these environmental factors, including light, air and soil temperature, influence the root regeneration potential and shoot growth of *P. radiata* seedlings after planting to the forest or after undercutting and/or wrenching in the nursery is the subject of subsequent chapters of this thesis.

CHAPTER 6

THE EFFECTS OF LIGHT INTENSITY AND PHOTOPERIOD ON THE ROOT REGENERATION POTENTIAL AND SHOOT GROWTH OF *Pinus radiata* SEEDLINGS

6.1 INTRODUCTION

Light is one of the most important factors governing the survival, growth and development of seedlings both in the nursery and once planted in the forest. Light affects plant growth through its intensity, duration and periodicity or photoperiod, and its quality (Shirley, 1929; Burkholder, 1936; Richardson, 1956 ; Kramer and Kozlowski, 1960; Bhatnagar, 1966; Leopold and Kriedemann, 1975). Variations in any of these light characteristics can modify the growth and development of seedlings (Burkholder, 1936; Nitsch, 1957a, b; Kramer and Kozlowski, 1960) which consequently influences timber quality and also the rotation period of the crop. Burkholder (1936) and Kramer and Kozlowski (1960), amongst others, review the effects of light on plant growth, including both the physiological and morphological changes that occur.

There is an extensive literature on the effects of light intensity on tree growth. Changes in light intensities have been shown to bring about marked morphological changes (Shirley, 1929, 1935, 1945; Pearson, 1936, 1940; Baker, 1945; Richardson, 1956 ; Logan, 1959, 1965, 1966, 1970; Kramer and Kozlowski, 1960; Krueger, 1967b; Krueger and Ruth, 1969; Wood, 1969; Fairbairn and Neustein, 1970; Loach, 1970; Brix, 1971, 1972; Eccher and Liani, 1972; Webb, 1976). Plant growth has been examined over a wide range of light intensities in the literature. In general, the higher light intensities of those reported have been observed to stimulate growth of the plant, resulting in:

a) a greater production of roots either in weight or length (Shirley, 1929, 1945; Biswell, 1935; Baker, 1945; Bieleski, 1959; Logan, 1959, 1965, 1966; Hellmers, 1963a; Steinbrenner and Rediske, 1964; Krueger, 1967b; Strothman, 1967; Lavender *et al.*, 1968; Logan and Krotkov, 1968; Wood, 1969; Fairbairn and Neustein, 1970; Brix, 1972; Eccher and Liani, 1972; Abod, 1977) and an increased rate of root elongation (e.g. Stone, 1967a; Webb, 1976).

b) an increase in stem diameter (Shirley, 1929; Logan, 1959, 1965, 1966; Fowler, 1961; Wood, 1969; Fairbairn and Neustein, 1970; Brix, 1972; Abod, 1977).

c) a decrease in height growth for some species (Shirley, 1929; Pearson, 1936, 1940; Hellmers, 1963a; Wood, 1969; Fairbairn and Neustein, 1970; Logan, 1970) or an increase in height for others (Logan, 1966; Fairbairn and Neustein, 1970).

d) an increase in the production of foliage (e.g. Krueger, 1967b; Logan and Krotkov, 1968) or leaf area (Logan, 1966, 1970; Logan and Krotkov, 1968).

e) an increase in oven dry weight of the stem and the root (Shirley, 1929, 1945; Baker, 1945; Logan, 1959; Hellmers, 1963a; Steinbrenner and Rediske, 1964; Lavender *et al.*, 1968; Fairbairn and Neustein, 1970; Brix, 1967, 1971, 1972; Abod, 1977) and of the foliage and branches (e.g. Shirley, 1929; Logan, 1966).

f) an increase in the root:shoot ratio (Shirley, 1929; Baker, 1945; Bieleski, 1959; Steinbrenner and Rediske, 1964; Krueger and Ruth, 1969; Fairbairn and Neustein, 1970).

Very marked differences between species have been reported. Species not only vary in the amount of light they require at different stages of growth but also in their response at different levels of light intensity (Fairbairn and Neustein, 1970).

Many factors contribute to the morphological changes that occur under varied light intensities. Perhaps the most important are the direct effects of light intensity on various physiological processes of the seedling including:

a) the rates of photosynthesis (Shirley, 1929; Kramer and Decker, 1944; Bourdeau and Laverick, 1958; Kramer and Kozlowski, 1960; Brix, 1967; Krueger, 1967b; Krueger and Ruth, 1969; Larcher, 1969; Rook, 1969c; Wood, 1969; Loach, 1967, 1970; Logan, 1970; Bleasdale, 1973; Devlin, 1975; Abod, 1977).

b) stomatal resistance (Zelitch, 1965; Logan and Krotkov, 1968; Turner, 1970, 1974; Wuenschner and Kozlowski, 1970, 1971; Woods and Turner, 1971; Davies and Kozlowski, 1974, 1975).

c) translocation of current photosynthates (Logan, 1959; Shiroya *et al.*, 1962; Nelson, 1963; Wardlaw, 1968).

d) chlorophyll synthesis (Shirley, 1929; Kramer and Kozlowski, 1960; Logan and Krotkov, 1968; Wood, 1969).

e) production of growth substances (Kozlowski and Peterson, 1962).

f) nitrogen metabolism (Shirley, 1935, 1945).

Alteration of natural light intensity is used to a limited extent in the production of seedlings in the nursery and establishment after planting. The use of shade in nurseries, for example, is a common practice in the production of some tree species (Stoeckeler and Jones, 1957; Schubert and Adams, 1971; Awang, 1973). The benefits of shading include conservation of soil moisture; maintenance of high humidity and therefore reduced transpiration of new germinants; reduction in extreme changes in temperature; reduced insolation and protection from birds, heat, and frost until seedlings become established (Schubert and Adams, 1971; Awang, 1973). Beyond this initial alteration in light and heat by shading no form of light modification is carried out on a large scale in nurseries, although containerized stock may frequently be held under high shade for considerable periods.

In Australia and New Zealand, nurseries of *P. radiata* are unshaded since sowing and germination normally take place in late winter, when the chance of heat and drought damage to seedlings is low. *P. radiata* is classed as intermediate in shade tolerance (Baker, 1949; Pawsey, 1953; Roy, 1966), and shade applied at this time would inevitably set back growth and result in much poorer quality stock (see Eccher and Liani, 1972). Reports by Huberman (1940) and Wakeley (1954) have pointed to the unfavourable effect on root development in shading southern pine nursery stock.

The daily duration of light (day-length) and even more importantly the length of night, affects the growth of many forest trees. In general, long days enhance seedling growth while short days inhibit growth and induce dormancy (Jester and Kramer, 1939; Wareing, 1948, 1950a,b, 1956; Downs and Borthwick, 1956; Kramer, 1957; Nitsch, 1957b; Vaartaja, 1957, 1959; Downs and Piringer, 1958; Bagley and Read, 1960; Kramer and Kozlowksi, 1960; Giertych and Farrar, 1961; McGregor *et al.*, 1961; Nienstaedt and Olson, 1961; Skok, 1961; Downs, 1962; Lavender *et al.*, 1968; Bhatnagar *et al.*, 1970; Wareing, 1971).

The striking effects of photoperiod on various vegetative and reproductive responses in woody species are well documented (see reviews by Wareing, 1948, 1956; Nitsch, 1957a; Kramer and Kozlowski, 1960; Fowler, 1961). The growth responses that are affected by

photoperiod, as cited by Wareing (1956), Nitsch (1957b) and Bhatnagar *et al.* (1970) include:

a) the extent of extension growth
b) duration of extension growth
c) time of leaf abscission
d) duration of cambial activity
e) induction and breaking of dormancy
f) leaf growth
g) flowering
h) seed germination.

Not only is the total growth of trees affected by day-length but also the distribution of growth between various parts of the seedling. Exposure of some species to long days, for example, stimulates the following growth patterns:

a) a much greater production of roots (Bonner, 1940; Fowler, 1961; Malajczuk, 1967; Hellmers and Pharis, 1968; Lavender and Wareing, 1972; Rook and Hobbs, 1972).

b) an increase in height growth (Jester and Kramer, 1939; Wareing, 1950a; Downs and Borthwick, 1956; Vaartaja, 1959; Bagley and Read, 1960; McGregor *et al.*, 1961; Jensen and Gatherum, 1965; Malajczuk, 1967; Hellmers and Pharis, 1968; Lavender *et al.*, 1968; Bhatnagar *et al.*, 1970; Florence and Malajczuk, 1970; Rook and Hobbs, 1972).

c) an increase in stem diameter (Skok, 1961; Bhatnagar *et al.*, 1970; Rook and Hobbs, 1972).

d) a stimulation in the growth of needles (Wareing, 1950a; Downs and Borthwick, 1956; Downs and Piringer, 1958; Fowler, 1961; Jensen and Gatherum, 1965; Bhatnagar *et al.*, 1970).

e) an increase in root:shoot ratio (e.g. Giertych and Farrar, 1961).

Details of the photoperiodic responses of trees, however, differ markedly with species and with different races and provenances of the same species (Garner and Allard, 1920; Jester and Kramer, 1939; Wareing, 1948, 1950a,b, 1956; Downs and Borthwick, 1956; Downs and Piringer, 1958; Vaartaja, 1957, 1959; McGregor *et al.*, 1961; Nienstaedt and Olson, 1961). The photoperiodic responses of many plant species are modified by temperature and some species require a chilling treatment to induce growth (e.g. Roberts and Struckmeyer,

1938, 1939, 1946, Gustafson, 1938; Wareing, 1956; Kramer, 1957; Bagley and Read, 1960; Cram and Lindquist, 1963; Jensen and Gatherum, 1965).

P. radiata behaves differently to many other species and appears to be less sensitive to photoperiod (Vaartaja, 1959; Rook, 1975). Shoot growth of *P. radiata* is significantly reduced with a short eight hour day compared to a long sixteen hour day, but it makes appreciable growth under short day-lengths and does not set dormant buds (Rook, 1975). In Australia and New Zealand *P. radiata* owes its great productivity to its ability to grow virtually throughout the year.

Investigations into the growth responses of *P. radiata* seedlings to photoperiod and light intensity are few. In terms of root regeneration potential of seedlings, no information is available.

The use of artificially lengthened photoperiods and various light intensities to test the growth responses of *P. radiata* appeared to be worth investigating. Information acquired for such work could be useful in devising and interpretating silvicultural practice both in the nursery and at the planting site. In the context of intensive seedling production the use of supplemental light to increase the rate and amount of growth of seedlings might be practical in some circumstances, such as in raising and possibly conditioning nursery stock in a comparatively short time. In the field, knowledge of the light requirements of the species could be useful in regard to underplanting or planting in cutovers bordered by standing timber.

Two experiments are detailed in this chapter. Experiment 1 was carried out to examine a) the shoot growth of intact *P. radiata* seedlings grown under various light intensities and b) the root regeneration potential and shoot growth of the preconditioned seedlings, three weeks after replanting under the same light intensities. Experiment 2 examined the effect of photoperiod on root regeneration potential and shoot growth of *P. radiata* seedlings, three weeks after planting.

6.2 MATERIALS AND METHODS

P. radiata seedlings (seed origin: Green Hills, S.F., N.S.W.) for both photperiod and light intensity experiments were raised in a Forestry Department glasshouse as described in Chapter 3 (Sections 3.2.1, 3.3.1, 3.3.3). Throughout this period an extended day-length of sixteen hours was provided by fluorescent tubes. When seedlings were ready for treatment, they were transferred to the CERES phytotron where they were fumigated with organo P before entry.

6.2.1 Experiment 1 - Light Intensity

Out of sixty seedlings (approximately six months old), twenty-one were carefully selected for the experiment, seven for each treatment. The experiment was conducted in three artificially-lit LB cabinets at CERES, set at the following light intensities:

LI_1 - 225$\mu Em^{-2}sec^{-1}$ (1000 f.c.)

LI_2 - 430$\mu Em^{-2}sec^{-1}$ (2000 f.c.)

LI_3 - 630$\mu Em^{-2}sec^{-1}$ (3000 f.c.)

The cabinets were run at a day/night temperature of $27^{o}/22^{o}C$ with a photoperiod of twelve hours.

The light source for the LB cabinets is twenty-eight V.H.O. (140 watt) fluorescent tubes - Philips T.L.M.F. 140/33 RS, supplemented by four incandescent lamps. The light canopy is sealed to exclude dust and arched to provide a uniform light intensity across the cabinet.

Light intensity was regulated by switching out pairs of fluorescent lights or by raising or lowering the platform in the cabinet which holds the trays of seedlings. The intensity of light was measured with a portable 'Eel' photoelectric photometer at five places in the cabinet (near the four corners and centre). The mean of the five values was recorded as the light intensity of the cabinet. Light intensity was checked at weekly intervals and corrected if it fell below the required level.

Seedlings with their root systems intact were allowed to grow for eighty-six days, under the various light intensities. At this time the seedlings were given regular applications of nutrient and water, shifted weekly to minimize the effect of position, and kept well-spaced to avoid mutual shading. After the eighty-six days stem diameters and heights were measured and the height growth of the

intact seedlings under the three light intensities was determined.

After the preconditioning period, all seedlings were carefully removed from the pots and regardless of root size pruned to 21 cm from the cotyledons. Any white root tips remaining after the pruning were pinched off before repotting. Once repotted seedlings were immediately returned to the cabinets and allowed to grow under the same light intensity in which they had been conditioned previously.

Three weeks later, all seedlings were harvested. Diameter and height increment, root regeneration potential, final dry weight of the shoot, regenerated root and total root, and root:shoot ratio were determined for all seedlings, as described in Chapter 3 (Section 3.4). The numbers of new white roots ≥ 0.5 cm (GT), ≥ 1.5 cm (LR) and 0.1-1.4 cm (SR) were counted and the lengths of LR (TL) were measured.

6.2.2 Experiment 2 - Photoperiod

From eighty seedlings (one hundred days old), twenty-four were carefully selected for treatment. The experiment was carried out in a naturally-lit C cabinet (see Chapter 3, Section 3.2.1) situated in an open glasshouse at CERES. Eight seedlings were placed into each of the three C units, each controlled for different photoperiods.

The photoperiods were:

P_{10} - ten hour photoperiod

P_{12} - twelve hour photoperiod

P_{16} - sixteen hour photoperiod

Seedlings in all treatments received eight hours of natural daylight and photoperiod extensions were provided by incandescent lamps. Air temperatures in the units were set for an eight hour, 27°C day and a sixteen hour, 22°C night. The eight hours of natural light were synchronized with the day temperature.

Seedlings were acclimatised for twelve days under the various photoperiods before their root systems were pruned and trimmed as outlined in Chapter 3 (Section 3.3.4). In brief, the roots were pruned to 21 cm from the cotyledons and any white root tips remaining were pinched off. Once repotted seedlings were returned to the C cabinets until harvested. During this treatment period seedlings were maintained as described in Chapter 3 (Section 3.3.3).

After four weeks, the diameter and height increment, root regeneration potential, final dry weight of the shoot, regenerated roots and total root and root:shoot ratio were determined for each seedling, as described in Chapter 3 (Section 3.4). Root regeneration potential was based on the number of new white roots $\geq$ 0.5 cm (GT), $\geq$ 1.5 cm (LR) and 0.5-1.4 cm (SR), and the length (TL) and average length (AL) of LR produced by each seedling.

6.3 STATISTICAL ANALYSIS

In both photoperiod and light intensity experiments, Duncan's multiple range test was used to test the differences between the treatment means. The differences for all parameters were tested at the 5% level of significance. Coefficients of variability were calculated for every parameter measured.

The results of the analyses of the light intensity and photoperiod experiments are presented in Tables 6.1 and 6.2, and Table 6.3 respectively.

6.4 RESULTS

6.4.1 Light Intensity

6.4.1.1 Height Growth of Intact Seedlings

Results presented in Table 6.1 show that height growth of intact seedlings was significantly affected by light intensity. After eighty-six days, seedlings under the lowest light intensities in treatments LI_1 and LI_2 were significantly taller than seedlings under the highest light intensity, LI_3. The height increments of seedlings in treatments LI_1 and LI_2 were not statistically different, but significantly greater than for seedlings in treatment LI_3. Height increments of seedlings in treatment LI_1, for example, were more than twice thoseof seedlings in treatment LI_3.

Unfortunately, stem diameter was not measured initially, however, as shown in Table 6.2, stem diameter after eighty-six days was significantly different between treatments. Stem diameter increased with increasing light intensity. The plants were of quite different form, as the shortest and stockiest of all the seedlings were in treatment LI_3, the tallest and more slender in treatment LI_1. The

Table 6.1 Height growth of intact *P. radiata* seedlings under 3 light intensities measured after 86 days. Treatments LI_1, LI_2 and LI_3 represent light intensities of 225 $\mu Em^{-2}sec^{-1}$ (1000 f.c.), 430 $\mu Em^{-2}sec^{-1}$ (2000 f.c.) and 630 $\mu Em^{-2}sec^{-1}$ (3000 f.c.) respectively.

Parameter	Treatment Mean[1] (C.V.)[2]		
Initial height (cm)	30.4(14.3) LI_3	33.2(32.2) LI_1	34.9(7.31) LI_2
Height after 86 days (cm)	37.96(14.8) LI_3	46.30(10.1) LI_2	51.00(12.1) LI_1
Height increment after 86 days (cm)	7.59(39.1) LI_3	11.44(29.8) LI_2	16.87(65.0) LI_1
Diameter after 86 days (mm)	10.00(5.9) LI_1	12.14(6.0) LI_2	13.63(8.5) LI_3

1 Mean of 8 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

Table 6.2 The effects of light intensity on the RRP and shoot growth of *P. radiata* seedlings measured 3 weeks after planting. Treatments LI_1, LI_2 and LI_3 represent 225 $\mu Em^{-2}sec^{-1}$ (1000 f.c.), 430 $\mu Em^{-2}sec^{-1}$ (2000 f.c.) and 630 $\mu Em^{-2}sec^{-1}$ (3000 f.c.) respectively.

Parameter	Treatment Mean[1] (C.V.)[2]		
Root Regeneration			
Number of new roots ≥0.5 cm (GT)	171(58.4) LI_1	246(49.3) LI_2	289(24.3) LI_3
Number of new roots ≥1.5 cm (LR)	102(66.4) LI_1	149(58.7) LI_2	192(26.2) LI_3
Number of new roots 0.5-1.4 cm (SR)	69(49.3) LI_1	95(25.1) LI_3	97(42.0) LI_2
Length of new roots ≥1.5 cm (TL) in cm	311.2(61.0) LI_1	543.3(76.0) LI_2	736.6(42.0) LI_3
Diameter and Height			
Initial diameter (mm)	10.00(5.9) LI_1	12.14(6.0) LI_2	13.63(8.5) LI_3
Diameter increment (mm)	0.22(>100.0) LI_2	0.51(69.9) LI_1	0.71(69.6) LI_3
Initial height (cm)	37.96(14.8) LI_3	46.3(10.1) LI_2	51.0(12.1) LI_1
Height increment (cm)	0.29(>100.0) LI_3	0.43(>100.0) LI_1	0.42(>100.0) LI_2
Final Dry Weight			
Shoot (g)	39.237(10.3) LI_1	61.953(17.3) LI_2	69.819(17.8) LI_3
Regenerated root (g)	0.113(45.7) LI_1	0.241(>100.0) LI_2	0.289(50.3) LI_3
Total root (g)	7.329(32.6) LI_1	11.396(16.5) LI_2	12.611(23.8) LI_3
Root:shoot ratio	0.19(14.6) LI_1	0.19(11.7) LI_2	0.21(19.2) LI_3

1 Mean of 7 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

stocky and slender appearance of the stems of seedlings in these light intensities were due directly to the diameter in proportion to the height.

6.4.1.2 Root Regeneration Potential

As indicated in Table 6.2, the seedlings under the highest light intensity, LI_3, showed the best root regeneration potential, but, the only significant differences were between the highest (LI_3) and lowest (LI_1) light intensity. For numbers of short new roots (SR), there was no significant difference between treatments. The length (TL) of roots in treatment LI_1 was less than half the TL in treatment LI_3.

6.4.1.3 Diameter and Height of Root-pruned Seedlings

As shown in Table 6.2, the initial diameter and height of seedlings differed between treatments due to the previous period of different light intensity, but, regardless of the seedling size, there were no significant differences in the diameter or height increments between the three light intensities during the treatment period of three weeks following root-pruning. Seedlings with the largest diameter initially in treatment LI_3 increased most in diameter and the tallest seedlings in treatment LI_1 increased most in height but these minor differences were not statistically significant.

6.4.1.4 Final Dry Weight

The light intensities examined had marked effects on the size and consequently the dry weights of the seedlings. Seedlings pre-conditioned and allowed to grow under the lowest light intensity had the lowest final shoot and total root dry weights. In general, the shoot and total root dry weight of seedlings increased with increasing light intensity, with the highest dry weights recorded in treatment LI_3. No differences were found in shoot and total root dry weights between treatments LI_2 and LI_3, but the differences between LI_2 or LI_3 and LI_1 were significant. The weight of new regenerated roots was not significantly different between treatments. Thus, the marked differences in total root dry weight can be attributed to the considerably smaller initial root size of seedlings kept at lower light intensities.

The root:shoot ratios of seedlings under all light intensity treatments were similar, despite the differences in seedling sizes and the amounts of root system actually removed at root-pruning. All seedlings, regardless of size were pruned to a predetermined length (c. 21 cm from the cotyledons), consequently the large seedlings with long root systems were actually more severely pruned than were the smaller seedlings.

6.4.2 Photoperiod

6.4.2.1 Root Regeneration Potential

The root regeneration potential of seedlings was not markedly influenced by the three photoperiods examined. All seedlings, regardless of day-length, produced large numbers (GT, LR, SR) and lengths (TL) of new roots (Table 6.3).

Although no significant differences were found in the number of new roots $\geq$ 1.5 cm (LR) produced between treatments, the greater LR and TL for seedlings in treatment P_{16}, suggests that longer days favour growth of longer roots. The differences in TL between treatments P_{12} and P_{10} were not significant, but TL produced by seedlings in treatment P_{16} was significantly greater than produced in treatment P_{12}. The average length of LR (AL) increased with an increase in day-length, with the shorter roots produced under the ten hour photoperiod. The highest number of new roots (GT) was produced by seedlings under a ten hour and sixteen hour photoperiod. The greater number of new roots 0.1-1.4 cm (SR) produced under the shortest day, P_{10}, accounts for the higher GT produced under the ten hour than sixteen hour day.

Regardless of the root parameter measured, seedlings under the twelve hour photoperiod showed the poorest growth. The low LR and SR produced by seedlingsin treatment P_{12} accounts for the lowest TL and GT of all the photoperiods examined.

6.4.2.2 Diameter and Height

Diameter growth of the seedlings was not affected by a ten, twelve or sixteen hour photoperiod. Diameter increment differences between treatments were not significant (Table 6.3).

Height increment, on the other hand, increased with an increase in photoperiod. Differences in height increment between

Table 6.3 The effects of photoperiod on the RRP and shoot growth of *P. radiata* seedlings measured 4 weeks after planting. Treatments P_{10}, P_{12} and P_{16} represent the 10, 12 and 16 hour photoperiod respectively.

Parameter	Treatment Mean[1] (C.V.)[2]		
Root Regeneration			
Number of new roots ≥0.5 cm (GT)	88(27.0) P_{12}	110(20.3) P_{16}	124(26.7) P_{10}
Number of new roots ≥1.5 cm (LR)	66(28.7) P_{12}	80(27.0) P_{10}	86(17.3) P_{16}
Number of new roots 0.5-1.4 cm (SR)	22(45.3) P_{12}	24(47.6) P_{16}	44(38.2) P_{10}
Length of new roots ≥1.5 cm (TL) in cm	360.2(36.0) P_{12}	415.1(32.4) P_{10}	515.9(11.8) P_{16}
Average length of new roots ≥1.5 cm (AL) in cm	5.1(0.1) P_{10}	5.5(24.4) P_{12}	6.6(13.3) P_{16}
Diameter and Height			
Initial diameter (mm)	2.41(5.8) P_{10}	2.38(5.5) P_{12}	2.48(8.1) P_{16}
Diameter increment (mm)	0.56(47.4) P_{12}	0.62(30.5) P_{10}	0.66(30.1) P_{16}
Initial height (cm)	13.95(8.4) P_{12}	13.96(13.6) P_{10}	15.09(8.8) P_{16}
Height increment (cm)	3.61(22.8) P_{10}	4.99(25.5) P_{12}	6.96(19.0) P_{16}
Final Dry Weight			
Shoot (g)	1.128(18.0) P_{10}	1.228(16.4) P_{12}	1.492(12.0) P_{16}
Regenerated root (g)	0.105(24.8) P_{12}	0.128(24.9) P_{10}	0.140(14.3) P_{16}
Total root (g)	0.313(14.4) P_{12}	0.392(15.9) P_{10}	0.397(5.8) P_{16}
Root:shoot ratio	0.26(4.3) P_{12}	0.27(5.4) P_{16}	0.35(12.3) P_{10}

1 Mean of 8 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

treatments were statistically significant. Seedlings in treatment P_{10} showed the poorest height increment, almost half that of seedlings in treatment P_{16}, which grew the most.

6.4.2.3 Final Dry Weight

Seedlings under the sixteen hour photoperiod had the highest shoot dry weight of the photoperiods examined. Shoot dry weights of seedlings under the ten and twelve hour photoperiod were similar, and significantly less than for seedlings under the sixteen hour photoperiod. This greater shoot weight in treatment P_{16} could be attributed to the greater (but not significantly different) initial diameter and height of these seedlings, as well as the increase in height during the treatment period. For this reason, the greater shoot weight may not be attributed solely to the effect of photoperiod.

The weight of regenerated root is significantly greater in treatment P_{16} than in P_{12}, which reflects the greater numbers and lengths of roots produced by seedlings in P_{16} than in P_{12}. Differences in regenerated root weight between treatments P_{12} and P_{10}, and treatments P_{10} and P_{16} were not significant.

Seedlings under the twelve hour photoperiod had the lowest root dry weights of all treatments. The dry weight of roots in treatments P_{10} and P_{16} were similar, and significantly greater than for seedlings in treatment P_{12}. The differences in regenerated root weight could account for the differences in the total root dry weights, however, the initial sizes of the root system may have been responsible. In viewing the differences in final dry weights it must be kept in mind that variability in the sizes and therefore dry weights of seedlings could mask the real effects of treatment. This is particularly so, if the effects of the treatment are not marked.

When harvested, seedlings under the ten hour photoperiod had the highest root:shoot ratio of all photoperiods, which reflects the greater root than height growth of these seedlings. Root:shoot ratios of seedlings in treatment P_{12} and P_{16} were the same, and significantly lower than for seedlings under the shorter day, P_{10}.

6.5 SUMMARY OF RESULTS

6.5.1 Experiment 1 - Light Intensity

(i) Marked differences were observed in the shoot growth of intact seedlings after being grown under various light intensity treatments. Height growth of seedlings was greatly reduced and stem growth markedly increased with an increase in light intensity.

(ii) Light intensity had a significant effect on the form and quality of seedling produced. On the basis of shoot length:shoot diameter ratio or shoot diameter alone, seedlings under the highest light intensity were sturdier than seedlings under low light. Seedlings in treatment LI_1 were more slender and etiolated in appearance.

(iii) Seedlings under the highest light intensity produced the greatest numbers (LR, GT) and length of new roots (TL), but only the differences between treatments LI_3 and LI_1 were significant. Differences in SR were not significant between treatments.

(iv) Regardless of the initial differences in seedling size, due to the different light intensities, diameter and height increments were not significantly different three weeks after root-pruning and -trimming.

(v) Light intensity had marked effects on dry matter production of seedlings. Shoot and total root dry weight of seedlings increased with increasing light intensity, with highest dry weight in treatments LI_3 and LI_2 and lowest in treatment LI_1.

(vi) The initial root size of seedlings under low light was considerably smaller than of seedlings in treatments LI_2 and LI_3.

(vii) Root:shoot ratios of seedlings in all treatments were similar at the end of the three week treatment period, despite initial size differences.

6.5.2 Experiment 2 - Photoperiod

(i) The root regeneration potential of seedlings was not markedly influenced by photoperiod. Root growth in all treatments was substantial four weeks after planting.

(ii) Slightly poorer root growth was shown under the twelve hour day in terms of numbers (LR, SR, GT) and length (TL) of new roots, as

compared to the sixteen hour day which favoured the proliferation of many new and especially long roots (LR, TL). Differences between treatments were not all significant (see Table 6.3).

(iii) The short ten hour day stimulated the production of a greater number of short roots (SR, AL) on seedlings. In terms of total number of new root produced (GT) no differences were found between treatments P_{10} and P_{16}.

(iv) Diameter growth was not significantly influenced by photoperiod over the four week treatment period.

(v) Height growth increased significantly with an increase in photoperiod. Seedlings under a sixteen hour day showed the best growth, those under a ten hour day the poorest.

(vi) The greatest dry matter production, in terms of shoot, total root and regenerated root was under the longest photoperiod. The shoot and total root dry weights of seedlings under the ten and twelve hour day were similar. The only differences in regenerated root weight were between treatments P_{12} and P_{16}.

(vii) At the end of four weeks seedlings under the short ten hour day had the highest root:shoot ratio of all treatments. Root:shoot ratios of seedlings under the twelve and sixteen hour photoperiod were similar.

6.6 DISCUSSION

On the basis of the results and within the limitations of the experimental conditions reported here, the following conclusions can be drawn:

a) light intensity has a significant effect on the growth and development of the shoot and the root of *P. radiata* seedlings.

b) growth of *P. radiata* seedlings is not extremely sensitive to changes in photoperiod.

Results from the light intensity experiment indicate that growth of intact and root-pruned seedlings is markedly reduced by low light intensities. Striking differences in size and form became evident in seedlings during both the preconditioning period and the post root-pruning treatment period, under the various light intensities. The most outstanding feature of the experiment was the relative distribution of growth between shoot and root under the highest and the lowest light intensity.

Stem elongation of seedlings with intact root systems varied inversely with light intensity while stem diameter was proportional to the intensity. Seedlings under low light were very slender in appearance, which was due directly to their superior height rather than due to reduced diameter. Seedlings under low light were characteristic of etiolated plants. Succulence under low light is favoured at the expense of strength and sturdiness, in agreement with reports by Shirley (1929), Pearson (1936), Logan (1970), Eccher and Liani (1972), and others. Consequently, seedlings under the highest light intensity, as these were more sturdy, were the better quality seedlings.

The responses observed in the morphological features of the seedlings to the light conditions imposed were similar to responses previously observed in *P. radiata* (Baker, 1945; Wood, 1969; Eccher and Liani, 1972) and other tree species. *P. radiata* seedlings have exhibited maximum height growth under shade (Baker, 1945; Wood, 1969) but greatest root growth with increasing light intensity (Baker, 1945; Wood, 1969; Eccher and Liani, 1972), all in direct agreement with results presented here.

Increased height growth of seedlings under low light, but poor development of root systems (in terms of dry weight, Table 6.2, i.e., total root weight minus regenerated root weight), suggests preferential growth of shoot over root under low light intensity. Under high light intensities, the reverse pattern of growth was observed.

Pruning the roots of seedlings altered both these patterns of growth distribution. Shoot growth was markedly checked by root-pruning under all the light intensities examined, even after three weeks seedlings showed little evidence of diameter and height growth. The physiological and morphological changes of the seedlings brought about by preconditioning under the various light intensities appeared to have little influence on the immediate shoot growth of seedlings following root-pruning. The proliferation of new roots was, however, favoured to the immediate growth of the shoot, a growth pattern previously observed in Chapter 5 in seedlings root-pruned, undercut and/or wrenched.

Higher light intensities enhanced the regeneration of greater numbers and lengths of new roots, which is in agreement with work reported on *Pinus strobus* L. (Logan, 1959), *Pinus ponderosa* Laws. (Steinbrenner and Rediske, 1964; Stone, 1967a), *Pseudotsuga menziesii* (Mirb.) Franco (Steinbrenner and Rediske, Krueger, 1967b), *Pinus resinosa* Ait. (Strothman, 1967), *Pinus caribaea* Mor. and *Pinus kesiya* Royle ex Gordon (Abod, 1977).

The differences in root growth between treatments may well have been somewhat different had similar proportions of the root system relative to the root size been removed. Pruning all the root systems to a predetermined length resulted in differences in the relative amount of root removed from seedlings and consequently differences in the size of the root system from which subsequent root growth would occur. As shown in Chapter 5, severity of pruning largely determines the extent of immediate root growth. The data presented therefore may be a response to both light intensity and the residual root system.

There is known to be a direct relationship between the rate of photosynthesis and light intensity, provided no other factor is limiting (e.g. Devlin, 1975). Any changes to the size of the plant or photosynthetic system would undoubtedly alter the rates of photosynthesis (Bleasdale, 1973). Recent investigations by Abod (1977) with *P. caribaea* and *P. keysia* seedlings (see also Chapter 9) show that the rate of photosynthesis declines and rate of dark respiration increases immediately after root-pruning, followed by a consistently low rate of photosynthesis for several weeks. Under 16% shade *P. caribaea* seedlings showed marked and sustained reductions in photosynthesis throughout the four week treatment period, with no signs of recovery to the original rates of photosynthesis. Seedlings under 50% and 100% sun showed higher rates of photosynthesis and dark respiration at the end of the four week period. The reduced shoot growth of seedlings observed in these experiments may be related directly to reduced rates of photosynthesis.

Some authors contend that changes in the rate of photosynthesis due to a change in light intensity would have a commensurate effect on the elongation of roots (Richardson, 1956; Webb, 1976). But, Krueger (1967) working with *Ps. menziesii* seedlings at low light intensities (i.e., 35-1050 f.c.) found that where photosynthesis

exceeded respiration production of new roots resulted, suggesting that current photosynthates played a major part in root production. Work by Shiroya *et al.* (1962) indicates that the translocation of current photosynthates to the roots is reduced in seedlings grown under low light intensities, which could account for poor production of roots under low light. Wood (1969) found that the rate of dark respiration was lowest for *P. radiata* seedlings grown under shade and that the needles of shade grown plants had a high photosynthetic capacity. The ability of *P. radiata* to maintain some photosynthetic activity under low light intensities could be the reason for the significant growth of seedlings even under the lowest light intensity examined in the present experiments.

The various growth responses of seedlings under different light intensities can also be attributed to changes in hormone production (e.g. Kozlowski and Peterson, 1962), nitrogen metabolism (e.g. Shirley, 1935, 1945), enzymic differences (e.g. Logan and Krotkov, 1968) and stomatal resistance (e.g. Shirley, 1945; Logan and Krotkov, 1968). To what extent these processes, and the rates of photosynthesis and dark respiration of root-pruned *P. radiata* are influenced by light intensity requires further investigation.

Under the light intensities examined, i.e, approximately 10-25% of maximum sunlight, it has been shown that *P. radiata* seedlings are capable of intercepting sufficient light energy to sustain growth. It seems that shading of *P. radiata*, although not commonly practiced in the nursery or in the forest, would inevitably lead to production of poor quality seedlings. But, as shown by the results of the experiment *P. radiata* seedlings are capable of substantial early root growth after root-pruning when raised and planted into light intensities as low as 10% of maximum sunlight (approximately $2500\mu Em^{-2}sec^{-1}$ for December-January in the Canberra area).

The lowest light intensities in the Canberra area occur in the winter months of June and July, at which time incoming daily radiation is approximately $1100\mu Em^{-2}sec^{-1}$. Seedlings raised and planted at $225\mu Em^{-2}sec^{-1}$, $430\mu Em^{-2}sec^{-1}$ and $630\mu Em^{-2}sec^{-1}$ in this experiment all showed a proliferation of new roots. Even at a light intensity of $225\mu Em^{-2}sec^{-1}$ which is almost one fifth the light intensity encountered in the field at the time of planting, *P. radiata* seedlings are capable of successfully regenerating a new root system.

The experimental seedlings received twelve full hours of constant light intensity under a day/night temperature of $27^{o}/22^{o}C$. Such conditions may in fact be much more favourable to the growth of seedlings than might at first appear. Seedlings in the nursery and forest would be subject to a shorter day-length (c. ten hours) with approximately only five hours of sunshine daily and would be subject to cooler air and soil temperatures. Total incoming solar radiation and low air and soil temperatures may therefore limit seedling growth in the winter months in the field more than might be inferred from this light intensity experiment.

The growth of *P. radiata* seedlings was altered little by photoperiod treatment. A greater number and length of long roots was found under the longest day-length of sixteen hours together with increased height growth. A greater number of short roots was found under the shortest day of ten hours.

The tendency for better growth of seedlings under the longest day-length agrees with previous investigations with *P. radiata* (Malajczuk, 1967; Florence and Malajczuk, 1970; Rook and Hobbs, 1972) and many other species, for example, *Picea pungens* Englem., *Pinus sylvestris* L. (Cram and Lindquist, 1963), *Tsuga canadensis* (L.) Carr. (Nienstaedt and Olson, 1961), *Sequoia gigantea* (Lindl.) Decne. (Skok, 1961) and *Pinus roxburghii* Sarg. (Bhatnagar *et al.*, 1970). Contrary to these results, Vaartaja (1959) found that *P. radiata*, together with a few other species, was not at all responsive to photoperiod. Growth responses under long and short days varied little for these species.

The results of this experiment, show that the number of new roots $\geq$ 1.5 cm (LR) produced by seedlings under the ten, twelve and sixteen hour day-lengths were statistically similar, but that the new roots $\geq$ 1.5 cm were longer under the sixteen hour day-length. This tendency for greater proliferation of longer roots under increased photoperiod has been previously observed by Fowler (1961) with intact *P. strobus* seedlings and by Lavender and Wareing (1972) with nursery lifted *Ps. menziesii* seedlings.

Interestingly, the greatest number of short roots (SR, new roots 0.5-1.4 cm) produced was by seedlings under the shortest day-length of ten hours, almost double the number of the other treatments. Because of this large number of short roots, the total number of new roots produced (GT, new roots $\geq$ 0.5 cm), favours the odd combination

of treatments P_{16} and P_{10}. The greater total number of new roots in treatment P_{10} arises because of the greater number of short roots and statistically similar amounts of long roots ($\geq$ 1.5 cm) produced under both P_{10} and P_{16}.

Greater numbers of short roots produced in treatment P_{10} indicate seedlings under short days have at least an equivalent potential if not a greater potential for root regeneration as seedlings grown under longer day-lengths. But, it is apparent from the observations of root lengths that longer days favour the extension of roots.

Longer day-lengths provide a longer period for the active photosynthesis resulting in increases in the quantity of photosynthetic material available for both shoot and root growth. However, seedlings in all treatments in this experiment received only eight hours of natural day light during which appreciable photosynthesis would occur. The supplemental illumination by low light intensity incandescent lamps (c. 50 f.c.) would not result in any significant photosynthesis for the remaining photoperiod. The greater shoot elongation of the seedlings under the longer photoperiod, therefore, is presumably the result of a photoperiodic effect rather than the effect of increased photosynthates.

The elongating influence of incandescent-filament light on the vegetative growth of woody plants is known, and has been attributed to the far red to red radiant energy emitted by incandescent lamps (Downs and Borthwick, 1956; Downs and Piringer, 1958; Downs, 1962). The plant's phytochrome system is known to trigger growth responses such as stem elongation upon exposure to this quality of light (Downs, 1962; Leopold and Kriedemann, 1975). The increased height growth of seedlings under the longest photoperiod would probably be the result of a greater absorption of red to far red light by the phytochrome system and a more efficient utilization of food produced.

The observed differences in the growth of seedlings may have been related to the availability of growth substances. Bonner (1940), Wareing (1948, 1956) and Lavender and Wareing (1972) suggest that the production of growth substances necessary for shoot or root growth is affected by day-length conditions to which the seedling is exposed. A higher level of growth substances in seedlings under long photoperiod (see Bonner, 1940; Wareing, 1948, 1956) could be responsible for the slightly improved root and height growth of seedlings grown under a sixteen hour day.

The results indicate that *P. radiata* seedlings are capable of proliferating new roots under the photoperiods encountered in the nursery and the forest in Australian latitudes, providing no other factors are limiting. At latitude 35°S (approximately), at which Canberra is situated, day-length varies from about fourteen hours in summer (December-January) to ten hours in winter (June-July), comparable to the photoperiods examined in this study. In the Canberra area, scheduling of undercutting and/or wrenching operations could be undertaken without consideration as to the length of day. Similarly, seedlings planted to the forest in winter would be capable of proliferating new roots immediately after planting unhampered by any inhibiting action of shorter days.

The day-length regimes were all conducted under a single day/night temperature regime, 27°/22°C. Such a temperature would be very different to the temperature conditions encountered during the shorter days of winter in the Australasian environment. Day/night air temperatures of 27°/22°C do not occur in the winter months, however, air temperatures near ground level may reach these temperatures for short periods during the day, perhaps when solar radiation (c. 1100$\mu Em^{-2} sec^{-1}$) reaches a daily maximum. This could favour significant photosynthesis. But soil temperatures would not rise to such an extent, and may then be the most important factor limiting seedling growth in winter and early spring.

From the results presented, it is shown that *P. radiata* seedlings in terms of root regeneration potential are not markedly affected by photoperiod, but, that there is a tendency for high light intensity to stimulate root extension growth more than low light intensity. However, other factors may become limiting under high light intensities. Temperature and moisture, for example, may have a critical effect on root regeneration potential and seedling growth. In subsequent chapters, under light conditions shown in these experiments to be quite favourable for root growth, the extent to which temperature influences the survival and early growth of seedlings is examined.

CHAPTER 7

THE EFFECTS OF VARIOUS COMBINATIONS OF AIR AND SOIL TEMPERATURE ON THE GROWTH OF ROOT-PRUNED SEEDLINGS

7.1 INTRODUCTION

The effects of both air and soil temperature on the root regeneration potential of seedlings reported for species other than *P. radiata* has been reviewed in Chapter 2.

Previous work with *P. radiata* (Shepherd, 1965; Malajczuk, 1967; Cremer, 1968; Rook, 1969c; Wood, 1969; Florence and Malajczuk, 1970; Macpherson, 1970; Hellmers and Rook, 1973) indicates that optimum air temperatures for growth of this species occurs under warm days (21^{o}-24^{o}C) and cooler nights. Hellmers and Rook (1973) showed that, although seedlings grown under warmer days (20^{o}-24^{o}C) and nights (17^{o}-23^{o}C) exhibited the greatest height growth, seedlings under the cooler day and night temperatures (below 23^{o}C) had the higher relative growth rates. These authors found that night air temperature was the most important daily temperature parameter affecting seedling growth. A cool night air temperature of 5^{o}C proved the most beneficial for seedling growth.

Macpherson (1970) found that root growth of both intact and root-pruned *P. radiata* seedlings was significantly affected by day and night temperature. Satisfactory root activity was observed in cool temperature regimes ($18^{o}/13^{o}$C, $24^{o}/19^{o}$C, $27^{o}/22^{o}$C) but not at a hot temperature regime ($33^{o}/28^{o}$C).

The effects of soil temperature on growth of *P. radiata* seedlings (Babalola *et al.*, 1968; Bowen, 1970) and rooted cuttings (Rook and Hobbs, 1975) have also been reported. One of the most outstanding effects of soil temperature on seedling growth is the greater production of roots at warm soil temperatures as compared to the cool soil temperatures. Bowen (1970) noted that soil temperatures of 25^{o}C favoured greater root and shoot growth in *P. radiata* seedlings than at soil temperatures of 15^{o}C.

From the literature, it is evident that most of the previous air and soil temperature studies on *P. radiata* have dealt with seedlings with intact root systems. The growth of root-pruned or lifted

seedlings under various combinations of day/night air and soil temperatures has not been examined in any great detail. Even though we might reasonably expect temperature to exert a similar influence on the subsequent growth of root-pruned seedlings as on the growth of undisturbed seedlings, the growth responses may well differ.

The purpose of this study was to ascertain the root regeneration potential and shoot growth of root-pruned *P. radiata* seedlings planted under various combinations of day and night air and soil temperatures. Thirteen experiments are described in this chapter. The following aspects of temperature were examined:

Experiment 1 - Five combinations of day/night air temperature with a constant differential between day and night temperature. Soil temperatures were not controlled separately.

Experiment 2 - Four combinations of day/night air temperature in the lower temperature range. Soil temperatures were not controlled separately.

Experiment 3 - Four combinations of day/night air temperature with an increasing differential between day and night temperatures. Soil temperatures were not controlled separately.

Experiment 4 to 13 - Four combinations of day/night air temperature, with the soil temperature controlled separately, at different temperatures.

7.2 THE EFFECTS OF VARIOUS AMBIENT DAY AND NIGHT TEMPERATURES

7.2.1 Materials and Methods

Seedlings (seed origin : Green Hills, S.F., N.S.W.) used in Experiments 1 and 3 were raised in the Forestry Department glasshouse. The facility and procedures used are outlined in Chapter 3 (Sections 3.2.1, 3.3.1, 3.3.3). When ready for treatment, the seedlings were transferred to the CERES phytotron where they were fumigated with organo P before entry.

7.2.1.1 Experiment 1 - Constant Differential between Day/Night Temperatures

Three weeks prior to treatment, sixty seedlings were placed into an open glasshouse at CERES controlled at a day/night

temperature of $24^{o}/19^{o}C$, which is considered within the optimum range for growth of *P. radiata* (e.g. Shepherd, 1965; Cremer, 1968; Malajczuk and Florence, 1970).

Forty seedlings were selected for treatment. The root systems of all seedlings were carefully removed from the pots, washed, pruned to 21 cm from the cotyledons and any white root tips remaining were pinched off (details in Chapter 3, Section 3.3.4). After re-potting eight seedlings were randomly selected and placed into each of the temperature treatments and allowed to grow further until the harvest.

The five temperature regimes chosen covered a range of day/night temperatures available in the open glasshouses at CERES. The treatment temperatures included:

T_1 $15^{o}/10^{o}C$

T_2 $21^{o}/16^{o}C$

T_3 $24^{o}/19^{o}C$

T_4 $27^{o}/22^{o}C$

T_5 $30^{o}/25^{o}C$

The differential between day and night temperatures of all treatments was $5^{o}C$. Mean air temperatures were controlled within $\pm 1.5^{o}C$ of the desired temperature. Day temperatures were maintained for eight hours and night temperatures for the remaining sixteen hours. Photoperiod was extended to sixteen hours by low intensity incandescent lighting. Further details of the facilities are outlined in Chapter 3 (Section 3.2.1).

Throughout the growing period seedlings were maintained as described in Chapter 3 (Section 3.3.3). Four weeks after root-pruning and-trimming the seedlings were harvested. The root regeneration potential, diameter and height increment, relative growth rate of diameter and height, final dry weight of the shoot, regenerated root and total root, and root:shoot ratio were determined for each seedling as described in Chapter 3 (Sections 3.3.5, 3.4). Root regeneration potential was based on the numbers of new white roots $\geq$ 1.25 cm (GT), $\geq$ 2.5 cm (LR), 1.25-2.4 cm (SR), the length (TL) and average length (AL) of new white roots $\geq$ 2.5 cm.

7.2.1.2 Experiment 2 - Decreasing Day/Night Temperatures in the Lower Temperature Range

Eighty seedlings (seed origin : Yarralumla, A.C.T.) were raised at the CERES phytotron in a glasshouse controlled at a day/night temperature of $21^{o}/16^{o}C$ (procedures and facilities detailed in Chapter 3). When 127 days old thirty-two seedlings of most uniform size were selected. Eight seedlings were assigned to each of the following day/night temperature treatments:

T_1 $21^{o}/16^{o}C$

T_2 $15^{o}/10^{o}C$

T_3 $11^{o}/6^{o}C$

T_4 $8^{o}/4^{o}C$

Temperatures $21^{o}/16^{o}C$ and $15^{o}/10^{o}C$ were obtained in open glasshouses and temperatures of $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ were provided by B-cabinets within the glasshouses. For details of both facilities see Chapter 3 (Section 3.2.1). In all treatments the day temperature was held for eight hours and natural light was extended to sixteen hours by incandescent lamps. Seedlings were maintained throughout the treatment period as described in Chapter 3 (Section 3.3.3).

All seedlings were acclimatised to the treatment temperature for six weeks prior to being root-pruned. Seedlings in treatments T_3 and T_4 were gradually acclimatised to reduced temperatures by being held under each temperature, (increasingly cooler) for three weeks prior to being transferred to the appropriate treatment temperature. The schedule used in acclimation, root-pruning and harvesting seedlings is included together with the age of seedlings in Table 7.1. As shown, seedlings in each treatment were different ages at the time of root-pruning.

After appropriate acclimation, the seedlings were root-pruned to 21 cm from the cotyledons and all remaining white root tips were pinched off (procedure detailed in Chapter 3, Section 3.3.4). After replanting seedlings were grown for another three weeks under the respective temperatures, then harvested. At the harvest, the RRP, diameter and height growth, dry weights of the shoot, regenerated root, total root, root removed and root:shoot ratio were determined for each seedling. Root regeneration potential was based on the

numbers of new white roots ≥ 0.1 cm (GT), ≥ 1.5 cm (LR), 0.1-1.4 cm (SR) and the length (TL) and average length (AL) of new roots ≥ 1.5 cm.

Table 7.1 Schedule of the transfer times, root-pruning and harvesting procedures carried out and the age of the seedlings used at each treatment.

Duration of Experiment	Age of Seedlings (days)	Procedure
Day 1	127	8 seedlings held at $21^{o}/16^{o}C$ (T_1) 24 seedlings transferred to $15^{o}/10^{o}C$ (T_2, T_3, T_4)
Week 3	148	8 seedlings at $21^{o}/16^{o}C$ root-pruned 8 seedlings held at $15^{o}/10^{o}C$ (T_2) 16 seedlings transferred to $11^{o}/6^{o}C$ (T_3, T_4)
Week 6	169	8 seedlings at $21^{o}/16^{o}C$ harvested 8 seedlings at $15^{o}/10^{o}C$ root-pruned 8 seedlings held at $11^{o}/6^{o}C$ (T_3) 8 seedlings transferred to $8^{o}/4^{o}C$ (T_4)
Week 9	190	8 seedlings at $15^{o}/10^{o}C$ harvested 8 seedlings at $11^{o}/6^{o}C$ root-pruned 8 seedlings held at $8^{o}/4^{o}C$ (T_4)
Week 12	211	8 seedlings at $11^{o}/6^{o}C$ harvested 8 seedlings at $8^{o}/4^{o}C$ root-pruned
Week 15	232	8 seedlings at $8^{o}/4^{o}C$ harvested

Diameter and height measurements were taken at three week intervals for the duration of each treatment to determine the effects of the reduced temperatures on both intact and root-pruned seedling growth. As determinations of root growth require destructive sampling, root growth of intact seedlings could not be ascertained.

7.2.1.3 Experiment 3 - Increasing Differential between Day/Night Temperatures

Thirty-two seedlings (approximately three months old) were carefully selected for treatment, eight for each of the four temperature regimes examined. The treatments included the following day/night temperatures:

T_1 $27^oC/22^oC$

T_2 $27^oC/19^oC$

T_3 $27^oC/16^oC$

T_4 $27^oC/10^oC$

Naturally-lit 'C' cabinets, as described in Chapter 3 (Section 3.2.1) provided the facilities for temperature control. Day temperatures were maintained for eight hours and night temperatures for the remaining sixteen hours. The natural daylight period was limited to eight hours by light proof shutters. Photoperiod extensions of two hours were provided by low intensity incandescent lamps.

Seedlings were acclimatised in their respective day/night temperature treatments, two weeks prior to root-pruning and-trimming. All root systems were pruned to 21 cm from the cotyledons and trimmed as detailed in Chapter 3 (Section 3.3.4). Once repotted the seedlings were allowed to grow for another four weeks under the various day/night temperature regimes. During this time seedlings were watered and fertilized as described in Chapter 3 (Section 3.3.3).

After the four week treatment period, the root regeneration potential, diameter and height increment, relative growth rate of the diameter and height, final dry weight of the shoot, regenerated root and total root, and root:shoot ratio were determined for each seedling as described in Chapter 3 (Section 3.3.5 and 3.4). The numbers of new white roots $\geq$ 0.5 cm (GT), $\geq$ 1.5 cm (LR) and 0.5-1.4 cm (SR) were counted, and the lengths (TL) and average lengths (AL) of new white roots $\geq$ 1.5 cm measured for every seedling. Because the seedlings in this experiment were much smaller than those in Experiment 1, the amount and lengths of new root produced were considerably less. As a result, shorter lengths were used to designate the short (SR) and long (LR) roots produced.

7.2.2 Statistical Analysis

In Experiment 1 and 3 the differences between treatment means of each parameter were compared using Duncan's multiple range test at the 5% level of significance. Coefficients of variability were calculated for each parameter. Results of the analyses of Experiment 1 and 3 are presented in Tables 7.2 and 7.6 respectively.

The mean and standard error for all the parameters measured for the root-pruned seedlings in Experiment 2 are presented in Table 7.3. Because of the differences in the age, size and acclimation history of seedlings at each treatment the differences between treatment means could not be compared. It was not possible to separate out the effects of each of these factors from the responses observed.

7.2.3 Results

7.2.3.1 Experiment 1

a) Root Regeneration Potential

The results presented in Table 7.2 show that the root regeneration potential of the seedlings was significantly influenced by the day and night temperature regime in which the seedlings were grown. Figure 7.1 shows the numbers and lengths of new roots produced under the various temperatures.

In terms of numbers (LR, GT) and lengths (TL, AL) of new roots produced, seedlings under the lowest temperature regime, $15^{o}/10^{o}C$, showed marked and significantly poorer root growth than seedlings under all other treatments. The highest temperature, $30^{o}/25^{o}C$, also resulted in poorer root growth of seedlings, but, differences in root growth between temperatures $30^{o}/25^{o}C$ and $21^{o}/16^{o}C$ or $24^{o}/19^{o}C$ were not significant.

In general, seedlings at temperatures $27^{o}/22^{o}$, $24^{o}/19^{o}$ and $21^{o}/16^{o}C$ had the best root growth. There was a tendency for the production of larger numbers (GT, LR, SR) and greater lengths (TL) of new roots by seedlings under the $27^{o}/22^{o}C$ temperature regime, but, the differences in these parameters between treatments $27^{o}/22^{o}$, $24^{o}/19^{o}$ and $21^{o}/16^{o}C$ were not always significant.

The greatest average length (AL) of long roots was found under the $24^{o}/19^{o}C$ temperature regime, but the AL at this temperature

Table 7.2 Effect of temperature on the root regeneration potential and shoot growth of *P. radiata* seedlings. T_1, T_2, T_3, T_4, T_5 represent day and night temperature regimes, 15/10, 21/16, 24/19, 27/22 and 30/25 °C respectively.

Parameter	Treatment Mean[1] (C.V.)[2]				
Root Regeneration					
Number of new roots ≥1.25 cm (GT)	84(51.8) T_1	182(38.4) T_5	235(40.4) T_3	278(30.0) T_2	323(38.6) T_4
Number of new roots ≥2.5 cm (LR)	41(64.4) T_1	117(37.5) T_5	175(31.9) T_2	176(43.1) T_3	200(44.2) T_4
Number of new roots 1.25-2.4 cm (SR)	43(48.0) T_1	59(42.2) T_3	65(43.4) T_5	103(43.4) T_2	123(30.0) T_4
Length of new roots ≥2.5 cm (TL) in cm	182.9(72.3) T_1	691.7(34.1) T_5	1018.2(38.8) T_2	1208.0(45.2) T_3	1309.5(38.4) T_4
Average length of new roots ≥2.5 cm (AL) in cm	4.24(12.1) T_1	5.72(12.1) T_2	5.95(8.2) T_5	6.70(11.4) T_4	6.90(8.5) T_3
Diameter and Height					
Initial diameter (mm)	4.40(7.2) T_1	4.50(15.7) T_5	4.55(12.4) T_4	4.58(6.7) T_2	5.01(15.7) T_3
Diameter increment (mm)	0.45(51.8) T_5	0.46(71.2) T_3	0.70(63.0) T_2	0.70(37.4) T_4	0.76(54.3) T_1
Relative growth rate diameter ($mm.mm^{-1}.day^{-1}$)	0.0029(75.9) T_3	0.0032(59.4) T_5	0.0045(55.6) T_2	0.0047(36.2) T_4	0.0052(44.2) T_1

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Table 7.2 (Cont'd)

Parameter	Treatment Mean[1] (C.V.)[2]				
Initial height (cm)	26.28(22.5) T_1	28.80(20.4) T_5	28.90(18.6) T_3	28.96(17.3) T_2	29.29(23.2) T_4
Height increment (cm)	0.71(41.4) T_1	2.70(70.2) T_3	3.15(45.4) T_2	4.09(40.4) T_5	4.15(48.0) T_4
Relative growth rate height ($cm.cm.^{-1}.day^{-1}$)	0.0011(36.5) T_1	0.0035(51.4) T_2	0.0043(44.2) T_5	0.0045(48.9) T_4	0.0074(>100.0) T_3
Final Dry Weight					
Shoot (g)	4.685(12.0) T_1	5.299(34.2) T_5	6.151(17.4) T_2	7.069(20.4) T_3	7.309(27.8) T_4
Regenerated root (g)	0.190(43.9) T_1	0.247(22.6) T_5	0.534(25.1) T_2	0.534(34.6) T_4	0.556(32.6) T_3
Total root (g)	1.514(19.5) T_1	1.822(33.1) T_5	1.962(29.8) T_4	2.271(30.8) T_2	2.669(19.7) T_3
Root:shoot ratio	0.27(9.5) T_4	0.32(11.5) T_1	0.36(17.0) T_5	0.37(11.7) T_2	0.38(7.8) T_3

1 Mean of 8 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

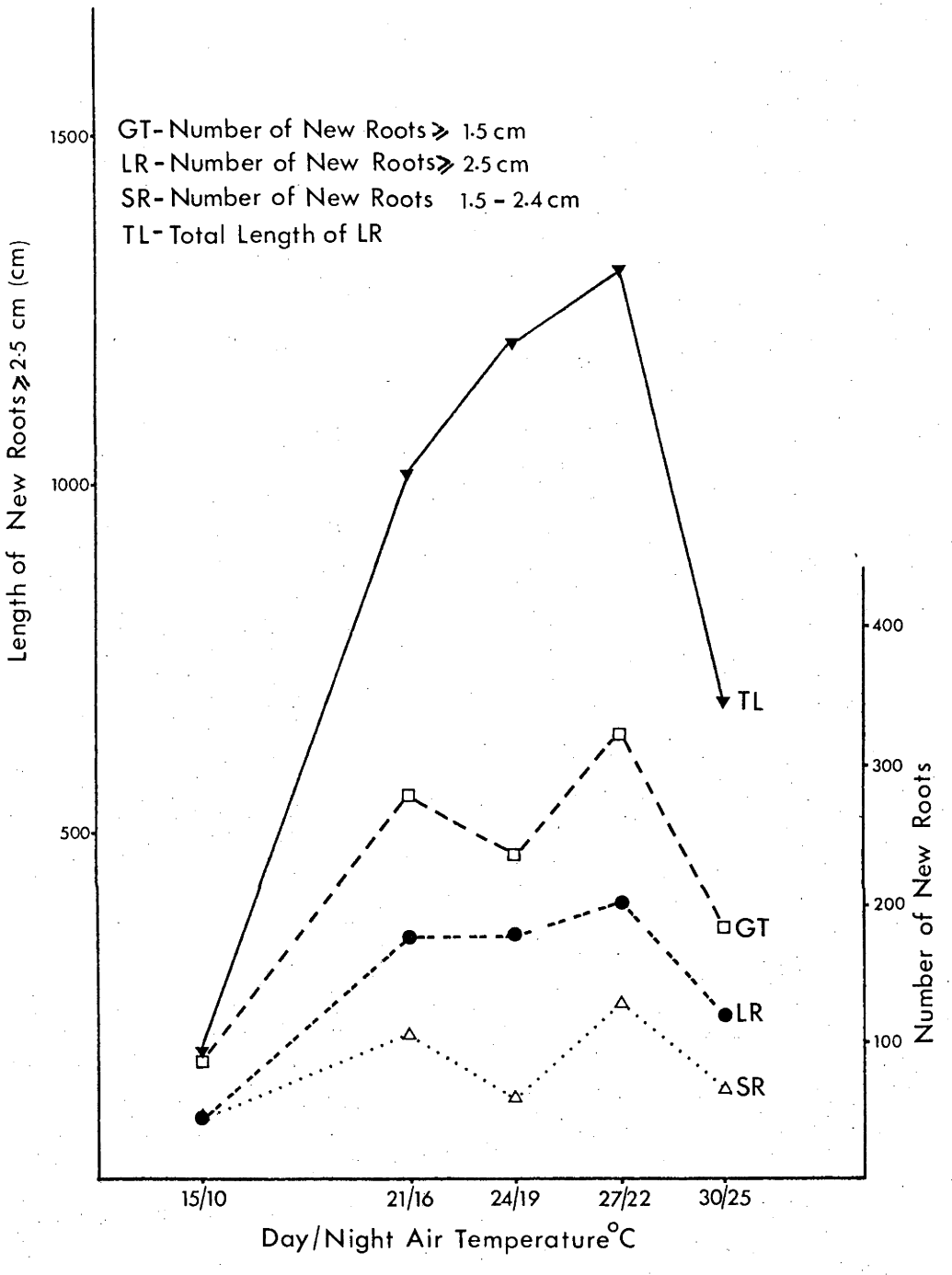

Figure 7.1. Effect of temperature on the root regeneration potential of *P. radiata* seedlings.

was not statistically different from that at $27^{o}/22^{o}C$. The longest of roots were produced at these temperatures, with significantly shorter roots produced under the cooler temperatures.

The numbers of short roots (SR) produced by seedlings in treatments $27^{o}/22^{o}C$ and $21^{o}/16^{o}C$ were almost twice those produced by seedlings at the other temperatures. Interestingly, the numbers of SR at $15^{o}/10^{o}C$ was almost equal to the numbers of LR, in contrast to the much greater numbers of LR than SR at the other temperatures.

The morphology of the new roots produced also differed with day/night temperature. New roots produced at the lower temperatures ($24^{o}/19^{o}C$, $21^{o}/16^{o}C$, $15^{o}/10^{o}C$) were much thicker and whiter in colour than those produced at the higher temperatures. Suberization of the new roots occurred at a faster rate at the higher temperatures of $27^{o}/22^{o}C$ and $30^{o}/25^{o}C$ than at the lower temperatures. Seedlings at $15^{o}/10^{o}C$ produced the thickest, whitest and most succulent roots, together with many initiating root "buds" (root primordia), too minute to be included in the root counts. Fewer initiating buds were found on seedlings at $21^{o}/16^{o}C$.

b) Diameter and Height

Temperature had no significant effect on diameter increment or relative rate of diameter growth (Table 7.2). Seedlings at the lowest temperature, however, grew the most in diameter and at a faster rate than seedlings at the other temperatures.

Height growth of seedlings was favoured under the highest temperature regimes, $30^{o}/25^{o}C$ and $27^{o}/22^{o}C$, however, the differences between these temperatures and temperatures $24^{o}/19^{o}C$ and $21^{o}/16^{o}C$ were not significant. The highest relative rate of height growth was recorded for seedlings under treatment $24^{o}/19^{o}C$ and this was significantly different from that of seedlings under treatment $15^{o}/10^{o}C$. No active lateral or terminal shoot elongation (new green growth) was observed on seedlings at $15^{o}/10^{o}C$.

Seedlings showed varying degrees of needle desiccation in all temperature treatments. This response to root-pruning was more pronounced at the higher temperatures, especially $30^{o}/25^{o}C$, than at $21^{o}/16^{o}C$ or $15^{o}/10^{o}C$.

c) Final Dry Weight

No significant differences were found in shoot dry weight between treatments $24^{o}/19^{o}C$ and $27^{o}/22^{o}C$, and treatments $15^{o}/10^{o}C$ and $30^{o}/25^{o}C$. The large diameter and height increment of seedlings under treatment $27^{o}/22^{o}C$ could account for the greatest shoot dry weight at this temperature. The lower shoot dry weights of seedlings under $15^{o}/10^{o}C$ could be the result of the slightly smaller initial size of the seedlings, as well as the poor height growth at this temperature.

The greatest dry weight of regenerated root was shown by seedlings at temperatures $21^{o}/16^{o}C$, $27^{o}/22^{o}C$ and $24^{o}/19^{o}C$, in general agreement with the larger numbers and lengths of new roots produced. Seedlings at $15^{o}/10^{o}C$ and $30^{o}/25^{o}C$ which showed the poorest root growth, had considerably less regenerated root dry weight than other seedlings.

The greatest total root dry weight, i.e., regenerated root weight plus residual root weight, of seedlings was found in temperatures $24^{o}/19^{o}C$ and $21^{o}/16^{o}C$. Although in general agreement with the dry weight of regenerated roots, differences in total root weight between treatments suggests variations in residual root after root-pruning.

Root:shoot ratios of seedlings in treatments $30^{o}/25^{o}C$, $24^{o}/19^{o}C$ and $21^{o}/16^{o}C$ were similar at the end of the four week treatment period. Seedlings in treatments $27^{o}/22^{o}C$ and $15^{o}/10^{o}C$ had significantly smaller root:shoot ratios.

7.2.3.2 Experiment 2

a) Root Regeneration Potential

Results in Table 7.3 and Figure 7.2 show that seedlings at temperatures as low as $8^{o}/4^{o}C$ still regenerated roots. However, root regeneration potential on the basis of length of new roots produced (Figure 7.3) was much lower at this temperature than any other.

The best root regeneration in terms of numbers (GT, LR, SR) and lengths (TL) of new roots was shown by seedlings under the $15^{o}/10^{o}C$ temperature regime. The reason for the poor response by seedlings under the $21^{o}/16^{o}C$ regime is most probably the effect of seedling age and size. Seedlings under the $15^{o}/10^{o}C$ temperature regime were much

Table 7.3 Effect of low temperatures on the root regeneration potential and shoot growth of root-pruned *P. radiata* seedlings. Treatment means[1] and standard errors of the means are presented for each parameter.

Parameter	Day/Night Air Temperature °C			
	21/16	15/10	11/6	8/4
Root Regeneration				
Number of new roots ≥0.1cm (GT)	21±6	134±23	49±11	86±14
Number of new roots ≥1.5cm (LR)	8±2	24±5	9±4	3±1
Number of new roots 0.1-1.4cm (SR)	13±4	110±20	40±8	83±13
Length of new roots ≥1.5cm (TL) in cm	22.1±6.4	55.4±11.4	21.1±7.9	6.7±2.6
Average length of new roots ≥1.5cm (AL)	2.06±0.51	2.23±0.08	1.91±0.28	1.64±0.25
Diameter and Height				
Diameter at root-pruning (mm)	5.04±0.06	6.36±0.16	6.78±0.13	6.93±0.14
Diameter at harvest (mm)	5.28±0.08	6.95±0.21	7.25±0.12	7.39±0.14
Diameter increment (mm)	0.24±0.05	0.60±0.11	0.47±0.04	0.46±0.04
Relative growth rate diameter ($mm.mm^{-1}.day^{-1}$)	0.0022±0.0004	0.0043±0.0007	0.0032±0.0003	0.0031±0.0003

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Table 7.3 (Cont'd)

Parameter	Day/Night Air Temperature ^{o}C			
	21/16	15/10	11/6	8/4
Height at root- pruning (cm)	30.18±1.40	31.49±1.22	30.74±0.53	31.20±0.99
Height at harvest (cm)	32.28±1.59	34.92±1.38	31.72±0.68	32.14±1.11
Height increment (cm)	2.10±0.35	3.44±0.68	1.02±0.17	0.94±0.16
Relative growth rate Height ($cm.cm^{-1}.day^{-1}$)	0.0032±0.0005	0.0049±0.0009	0.0016±0.0003	0.0023±0.0008
Final Dry Weight				
Shoot (g)	8.168±0.502	15.050±0.960	14.025±0.698	16.958±0.906
Regenerated root (g)	0.024±0.006	0.116±0.020	0.031±0.008	0.056±0.010
Total root (g)	1.821±0.115	3.955±0.234	4.411±0.177	5.706±0.238
Root removed at pruning (g)	0.357±0.043	0.819±0.052	1.110±0.067	1.585±0.153
Root:shoot ratio	0.22±0.01	0.26±0.01	0.31±0.02	0.33±0.02

1 Mean of 8 replicates.

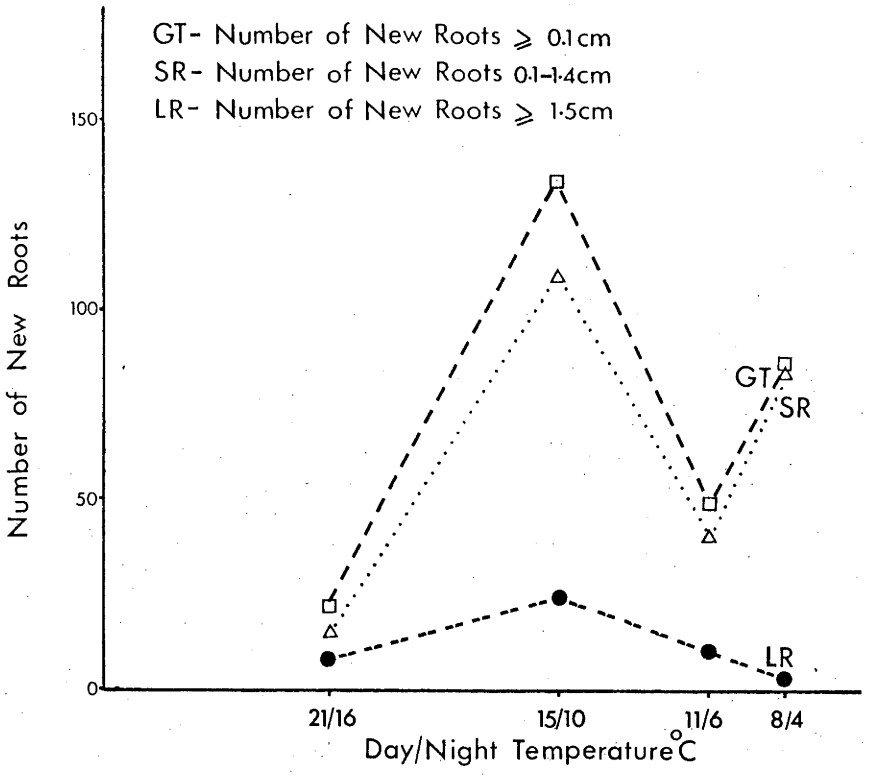

Figure 7.2. Effect of low temperature on the numbers of new roots produced by seedlings three weeks after root-pruning.

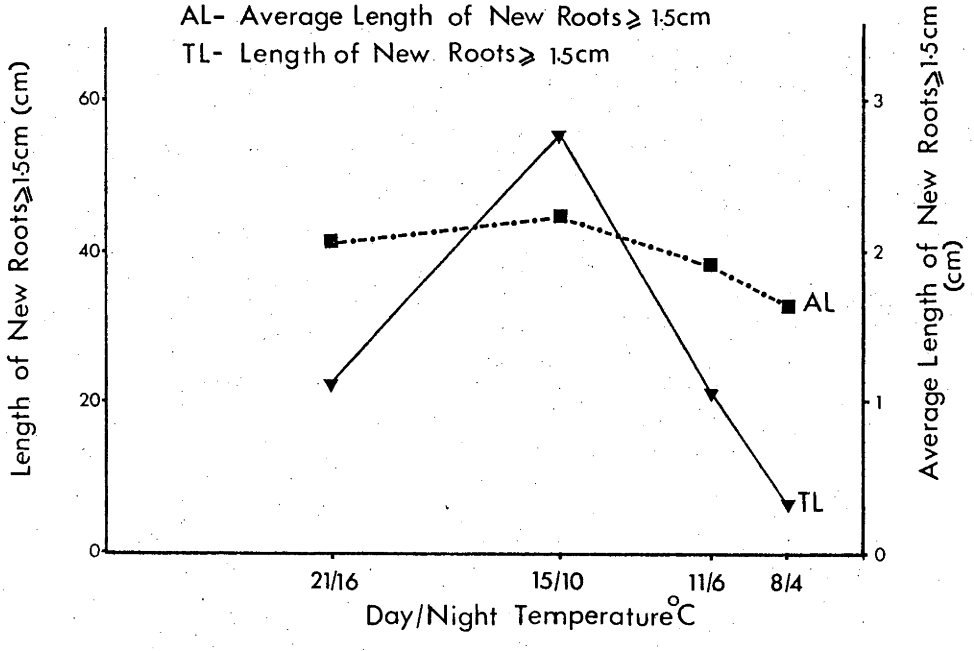

Figure 7.3. Effect of low temperature on the length of new roots produced by seedlings three weeks after root-pruning.

larger than those under the $21^{o}/16^{o}C$ temperature at the time of root-pruning (Table 7.3). A greater residual root after root-pruning with more growing points available for subsequent root growth would have resulted in such a response at $15^{o}/10^{o}C$, a temperature which although much lower than optimum still stimulates active root growth (see Experiment 1, Section 7.2.3.1). A preliminary experiment carried out at a temperature above $15^{o}/10^{o}C$ had shown that root regeneration potential increases with increasing age and size of seedlings. It would, therefore, be safe to assume that the age and size of seedlings in this experiment would have had some, if not an exactly similar influence, at the lower temperatures examined here.

Temperatures of $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ resulted in a much lower number of roots (GT, LR, SR) produced. Again, the greater production of roots at $8^{o}/4^{o}C$ than $11^{o}/6^{o}C$ could be due to the larger seedlings under the $8^{o}/4^{o}C$ than $11^{o}/6^{o}C$ temperature regime.

Temperature had a marked affect on the production of long roots (LR, TL, AL). Seedlings in all treatments produced a greater proportion of short (SR) than long (LR) roots (Figure 7.2 and 7.3). The proportion of SR to LR, however, increased with decreasing temperature. The number of LR produced by seedlings under the $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ temperatures was much lower than under the $15^{o}/10^{o}C$ temperature. The total length (TL) and average length (AL) of new long roots (LR) was also lowest at the lower temperatures (Figure 7.3), indicating that these temperatures were not at all favourable for extension of roots. The AL of LR produced under the $15^{o}/10^{o}C$ and $21^{o}/16^{o}C$ temperature regime were not markedly different, but, the greater proportion of SR to LR produced under the $15^{o}/10^{o}C$ temperature (approximately 81%) than under the $21^{o}/16^{o}C$ temperature (approximately 62%) suggests that the subsequent extension of new roots may be inhibited by the cooler $15^{o}/10^{o}C$ temperature.

All the new roots produced by seedlings under the $15^{o}/10^{o}C$, $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ temperature regimes were thick, succulent and white in colour. Under the $21^{o}/16^{o}C$ temperature regime the roots were relatively thinner, some were light brown in colour.

b) Height and Diameter

The diameter and height measurements of intact seedlings at each preconditioning temperature prior to root-pruning are presented

in Table 7.4. The corresponding diameter and height increments and relative growth rates of these seedlings in response to the changes in temperature are presented in Table 7.5. The diameter and height increment of seedlings in each treatment prior to and following root-pruning are illustrated in Figures 7.4 and 7.5 respectively.

Shoot growth of both intact and root-pruned seedlings was reduced, but not completely inhibited by low temperatures. In all cases, transferring intact seedlings to lower temperatures reduced growth substantially. Height was affected more by a drop in temperature than diameter growth. Both diameter and height growth were reduced markedly when intact seedlings were transferred from $15^{o}/10^{o}C$ to $11^{o}/6^{o}C$, with the poorest growth recorded for seedlings under the $8^{o}/4^{o}C$ temperature.

Root-pruning markedly reduced the diameter and height growth of seedlings under the $21^{o}/16^{o}C$, $15^{o}/10^{o}C$ and $11^{o}/6^{o}C$ temperature regimes (Table 7.3, Figure 7.4 and 7.5). The greatest reduction in diameter and height growth due to root-pruning occurred at the highest temperatures. Under the $8^{o}/4^{o}C$ temperature, height growth was reduced, but, diameter growth increased slightly with root-pruning. Diameter growth for root-pruned seedlings was lowest under the $21^{o}/16^{o}C$ temperature, but, this response may have been due to these being the youngest and smallest seedlings. Height growth, on the other hand, was higher for these seedlings than for those under the $11^{o}/6^{o}C$ or $8^{o}/4^{o}C$ temperature. Seedlings at $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ showed poorer shoot growth than seedlings at $15^{o}/10^{o}C$, which grew the most in diameter and height. The rates of diameter and height growth of seedlings at the two lower temperatures were virtually the same.

The health of the seedlings appeared to be affected by the lower temperatures. All seedlings under the $8^{o}/4^{o}C$ temperature looked unhealthy; their needles were dull and yellow-green in colour. With increases in temperature the needles of seedlings were dark glossy green. Seedlings in all treatments had desiccated needles.

c) Final Dry Weight

It was not surprising to find that the final dry weights of the shoot and total root of seedlings differed between treatments because of differences in the ages and sizes of seedlings used for RRP determination (Table 7.3). At harvest seedlings in treatment T_4 had

Table 7.4 Stem diameter and height of intact seedlings when gradually subjected to lower temperatures. Means and standard errors of the means are presented. Arrows indicate the seedlings (8 replicates per mean) that were transferred to the next lowest temperature.

Parameter	Day/Night Air Temperature (^{o}C)							
	$^{21}/_{16}$		$^{15}/_{10}$		$^{11}/_{6}$		$^{8}/_{4}$	
	A	B	C	D	C	D	C	D
Stem Diameter (mm)	3.68±0.06	5.04±0.06						
	3.67±0.06 →		4.79±0.10	6.36±0.16				
	3.65±0.05 →		4.90±0.05 →		5.73±0.08	6.78±0.13		
	3.66±0.06 →		4.87±0.09 →		5.76±0.08 →		6.63±0.15	6.93±0.14
Stem Height (cm)	19.20±0.58	30.18±1.40						
	18.71±0.49 →		24.26±0.76	31.48±1.22				
	18.98±0.49 →		25.09±0.49 →		27.91±0.59	30.74±0.53		
	18.89±0.54 →		24.87±0.73 →		27.71±0.79 →		30.05±0.89	31.20±0.99

A = diameter and height of seedlings raised under $^{21^{o}}/_{16^{o}C}$, measured at the commencement of the experiment.

B = diameter and height of seedlings measured 3 weeks after the commencement of the experiment.

C = diameter and height of seedlings 3 weeks after being transferred to the temperature indicated.

D = diameter and height of seedlings 6 weeks after being transferred to the temperature indicated.

Table 7.5 Diameter and height growth of intact seedlings in response to changes in temperature 3 weeks after transfer. Means (8 replicates per mean) and standard errors of the means are presented. Arrows indicate temperatures seedlings were transferred to in treatments T_1, T_2, T_3 and T_4.

Treatment	Temperature (°C)	Diameter increment (mm)	Relative rate of diameter growth ($mm.mm^{-1}.day^{-1}$)	Height increment (cm)	Relative rate of height growth ($cm.cm^{-1}.day^{-1}$)
T_1	21/16*	1.37±0.08	0.0151±0.0009	10.99±0.90	0.0214±0.0010
T_2	21/16→15/10	1.12±0.12	0.0115±0.0019	5.60±0.31	0.0122±0.0005
T_3	21/16→15/10	1.24±0.06	0.0140±0.0006	6.11±0.29	0.0134±0.0007
T_4	21/16→15/10	1.20±0.05	0.0135±0.0005	5.99±0.36	0.0131±0.0007
T_2	15/10*	1.56±0.08	0.0134±0.0004	7.22±0.60	0.0123±0.0008
T_3	15/10→11/6	0.83±0.04	0.0075±0.0003	2.78±0.17	0.0050±0.0005
T_4	15/10→11/6	0.89±0.04	0.0081±0.0004	2.84±0.27	0.0052±0.0005
T_3	11/6*	1.05±0.10	0.0080±0.0007	2.82±0.36	0.0046±0.0006
T_4	11/6→8/4	0.87±0.77	0.0067±0.0005	2.34±0.20	0.0038±0.0003
T_4	8/4*	0.30±0.02	0.0021±0.0001	1.15±0.21	0.0018±0.0003

* Seedlings held for 3 weeks at the temperature indicated.

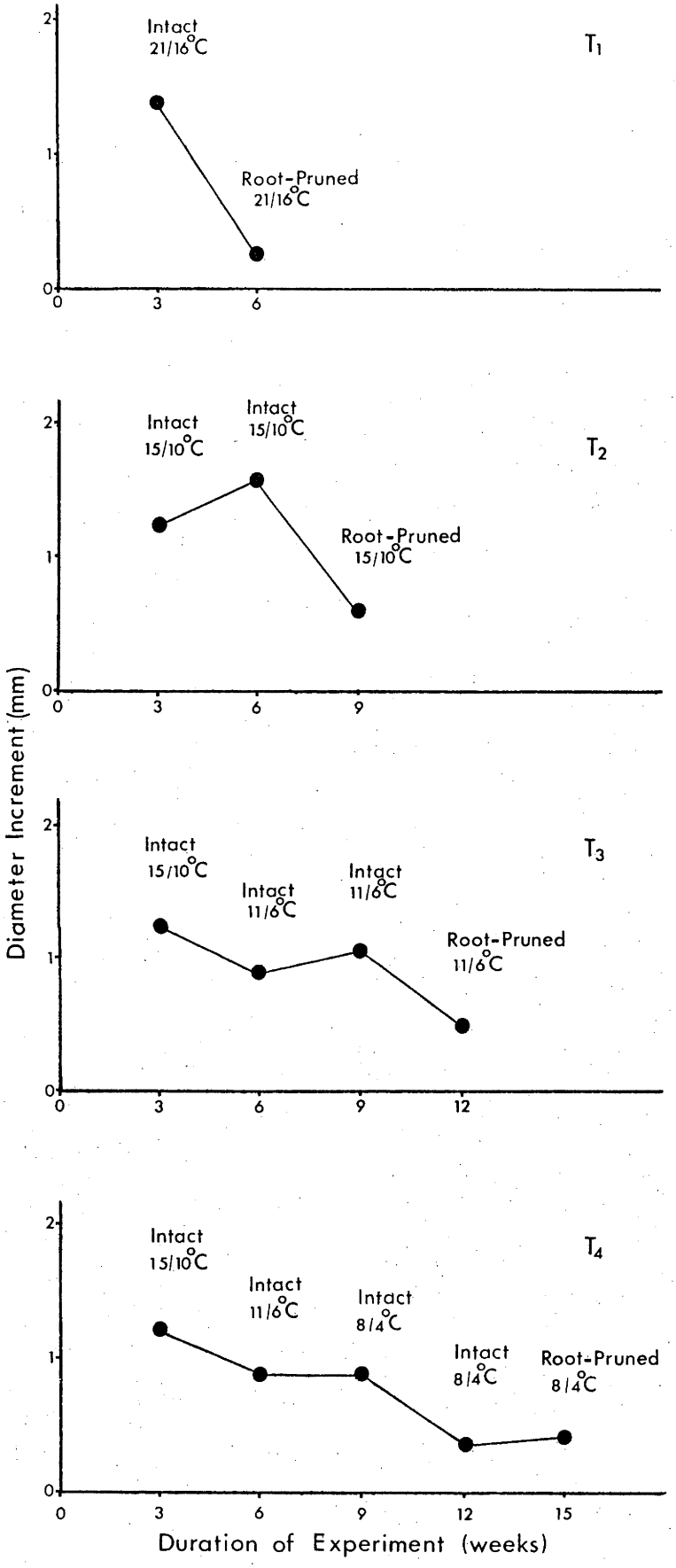

Figure 7.4. Diameter increment of intact seedlings gradually subjected to low air temperatures and of root-pruned seedlings at temperatures $21^{0}/16^{0}C$, $15^{0}/10^{0}C$, $11^{0}/6^{0}C$ and $8^{0}/4^{0}C$, represented by T_1, T_2, T_3 and T_4 respectively.

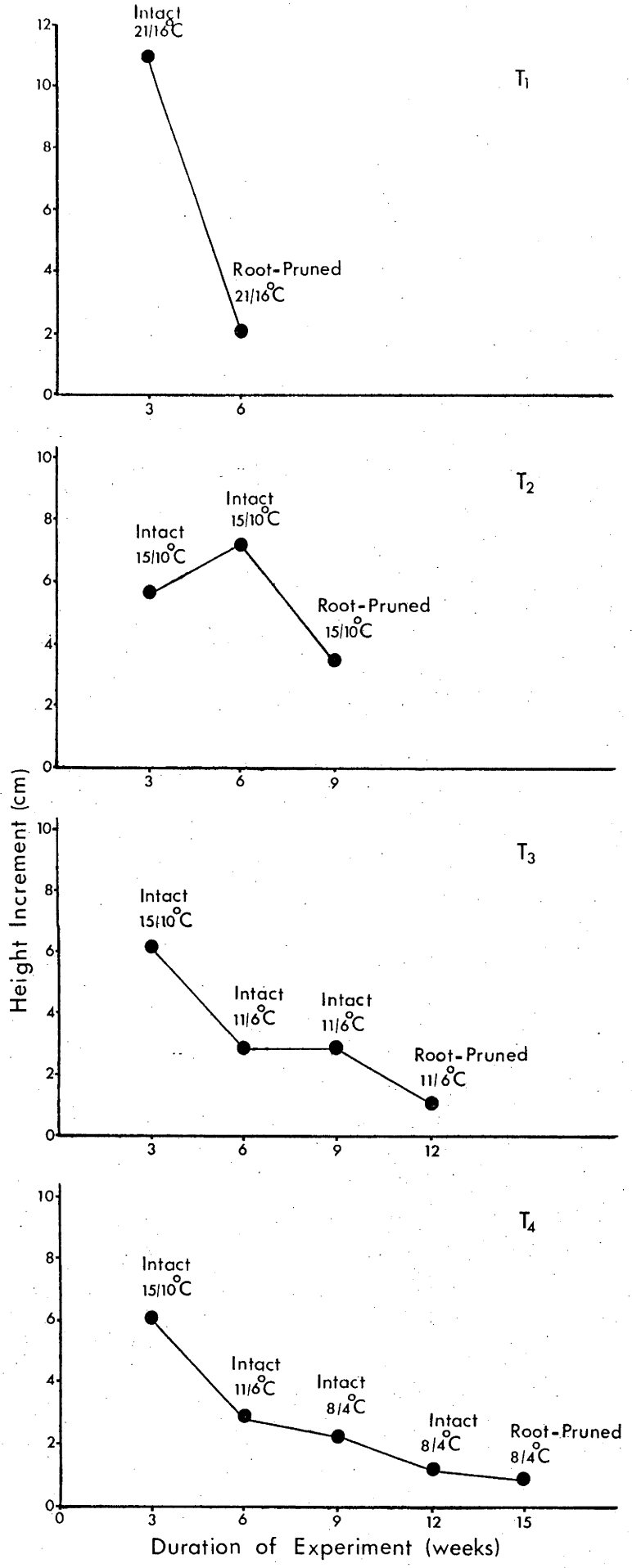

Figure 7.5. Height increment of intact seedlings gradually subjected to low air temperatures and of root-pruned seedlings at temperatures $21^{o}/16^{o}C$, $15^{o}/10^{o}C$, $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ represented by T_1, T_2, T_3 and T_4 respectively.

over twice the amount of shoot and almost three times the amount of total root (by weight) than seedlings in Treatment T1. The regenerated root dry weights are closely related to the numbers and lengths of new root produced.

The root:shoot ratios of the root-pruned seedlings differed between treatments, the differences due to acclimation and age rather than three weeks growth after root-pruning. Seedlings under the $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ temperature regimes had slightly higher root:shoot ratios than seedlings under the $21^{o}/16^{o}C$ and $15^{o}/10^{o}C$ temperatures.

7.2.3.3 Experiment 3

a) Root Regeneration Potential

The results presented in Table 7.6 and Figure 7.6 show that decreasing night temperature had no significant effect on the number of new long roots (LR) or the total number of new roots (GT) produced by seedlings. However, the lowest night temperature ($10^{o}C$) stimulated the production of greater numbers of short roots (SR) than the night temperatures of $19^{o}C$ or $22^{o}C$. Differences in SR between the $10^{o}C$ and $16^{o}C$ night temperatures were not significant. This greater proliferation of SR under the cool nights accounts for the larger though not significantly different, total number of roots (GT) found at these temperatures. The major proportion of all roots formed under the $10^{o}C$ night temperature were SR rather than LR. All other temperatures scored had more LR than SR.

There was a tendency for greater numbers of long roots (LR) to be produced under the warmer night temperatures of the $27^{o}/16^{o}C$ and $27^{o}/22^{o}C$ temperature regimes. The greatest length of LR (TL) was produced by seedlings under the warmest night temperature of $22^{o}C$, while seedlings under the coolest night produced the shorter LR. Differences in TL between treatments $27^{o}/19^{o}C$ and $27^{o}/22^{o}C$, and treatments $27^{o}/10^{o}C$ and both $27^{o}/16^{o}C$ and $27^{o}/22^{o}C$ were significant. The greater number of LR produced by seedlings in $27^{o}/16^{o}C$ accounts for the greater length of LR measured in $21^{o}/16^{o}C$ as compared to $27^{o}/19^{o}C$.

The average length of LR (AL) tended to decrease with decreasing night temperature, with the greatest AL at the $22^{o}C$ night more than twice the AL of roots at $10^{o}C$. Differences in AL between the $16^{o}C$ and $19^{o}C$ night were not significant, but significantly greater than under the $10^{o}C$ night.

Table 7.6 Effects of decreasing night temperature on the root regeneration potential and shoot growth of *P. radiata* seedlings. T_1, T_2, T_3, T_4 represent day and night temperature regimes, 27/22, 27/19, 27/16 and 27/10 °C respectively.

Parameter	Treatment Mean[1] (C.V.)[2]			
Root Regeneration				
Number of new roots ≥0.5 cm (GT)	124(26.7) T_1	127(31.7) T_2	152(42.6) T_3	161(24.8) T_4
Number of new roots ≥1.5cm (LR)	66(40.0) T_2	67(38.8) T_4	80(27.0) T_1	86(40.3) T_3
Number of new roots 0.5-1.4 cm (SR)	44(38.2) T_1	61(35.6) T_2	66(53.1) T_3	94(33.5) T_4
Length of new roots ≥1.5 cm (TL) in cm	170.0(51.2) T_4	274.9(41.0) T_2	388.2(43.8) T_3	415.1(324) T_1
Average length of new roots ≥1.5cm (AL) in cm	2.43(12.9) T_4	4.16(11.7) T_2	4.49(14.5) T_3	5.12(8.3) T_1
Diameter and Height				
Initial diameter (mm)	2.25(6.3) T_2	2.30(2.3) T_4	2.35(6.8) T_3	2.41(5.6) T_1
Diameter increment (mm)	0.60(30.0) T_4	0.62(49.7) T_2	0.62(39.0) T_3	0.62(30.5) T_1
Relative growth rate diameter ($mm.mm^{-1}.day^{-1}$)	0.0082(25.6) T_4	0.0083(31.3) T_1	0.0084(38.1) T_3	0.0086(47.7) T_2
Initial height (cm)	12.98(7.0) T_2	13.42(10.1) T_4	13.69(7.6) T_3	13.96(13.6) T_1
Height increment (cm)	2.65(33.8) T_3	3.36(19.0) T_2	3.61(22.8) T_1	4.99(43.7) T_4
Relative growth rate height ($cm.cm^{-1}.day^{-1}$)	0.0063(31.7) T_3	0.0082(14.6) T_2	0.0083(21.7) T_1	0.0113(44.2) T_4
Final Dry Weight				
Shoot (g)	0.960(18.6) T_4	0.970(13.9) T_2	1.128(18.0) T_1	1.169(13.9) T_3
Regenerated root (g)	0.065(46.2) T_4	0.070(34.8) T_2	0.089(33.4) T_3	0.128(25.0) T_1

(Cont'd next page)

Table 7.6 (Cont'd)

Parameter	Treatment Mean[1] (C.V.)[2]			
Total root (g)	0.261(21.8) T_4	0.270(22.1) T_2	0.283(16.0) T_3	0.392(15.9) T_1
Root:shoot ratio	0.24(9.4) T_3	0.27(7.9) T_4	0.28(8.6) T_2	0.36(12.3) T_1

1 Mean of 8 replicates.

2 C.V. = Coefficient of Variability in per cent.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$.

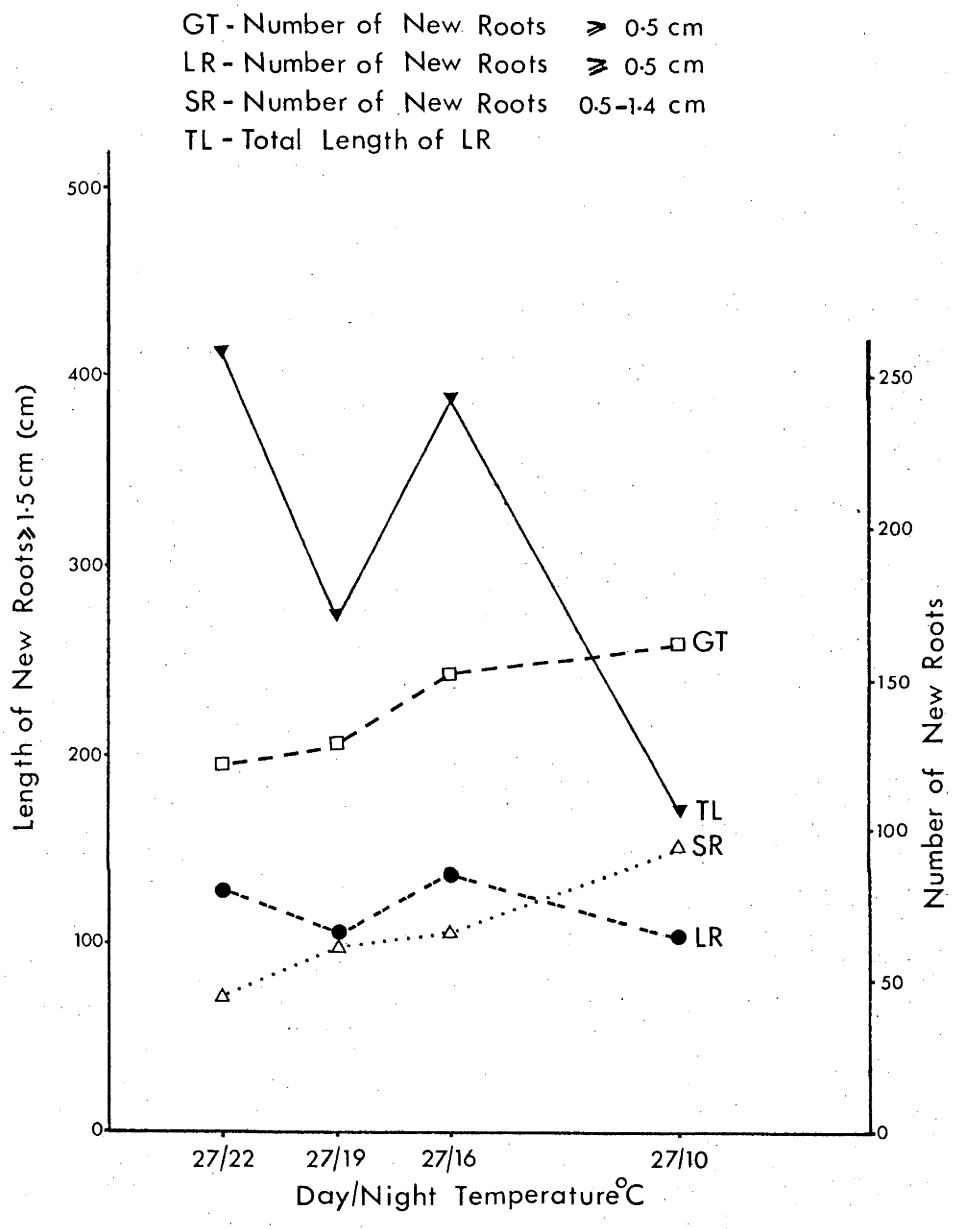

Figure 7.6. Effect of decreasing night temperature on the root regeneration potential of *P. radiata* seedlings.

The morphology of the newly regenerated roots was influenced by the different temperatures. Roots produced under the coolest ($10^{o}C$) night temperature were thick, succulent and white in colour. An increase in night temperature from $16^{o}C$-$22^{o}C$ resulted in the production of thinner, brown (suberized) roots. Roots at $16^{o}C$ were slightly whiter and thicker than roots at either the $19^{o}C$ or $22^{o}C$ night temperatures.

b) Diameter and Height

The diameter increments and relative rates of diameter growth of seedlings four weeks after pruning were similar, regardless of the temperature regime in which they were grown (Table 7.6).

The greatest height increment of seedlings occurred at the coolest night temperature of $10^{o}C$, however, the relative rate of height growth of these seedlings was only significantly greater than for seedlings under a $16^{o}C$ night. Increases in seedling height at temperatures $27^{o}/22^{o}C$, $27^{o}/19^{o}C$ and $27^{o}/16^{o}C$ were not significantly different. Seedlings in all treatments had desiccated needles. The only observed difference between treatments was in the more pronounced desiccation at $27^{o}/10^{o}C$ than at $27^{o}/22^{o}C$.

c) Final Dry Weight

The shoots of seedlings grown under a $16^{o}C$ night were significantly heavier than seedlings under the $10^{o}C$ or $19^{o}C$ night (Table 7.6). Despite the greatest height increment of seedlings in treatment $27^{o}/10^{o}C$ shoot weights were the lowest.

Seedlings under the warmest night had significantly greater dry weights of regenerated root and total root, which agree with the greater production of roots (TL) by these seedlings. Differences in total root and regenerated root dry weights between treatments $27^{o}/10^{o}C$, $27^{o}/16^{o}C$ and $27^{o}/19^{o}C$ were not significant.

Root:shoot ratios were greater for seedlings at $27^{o}/22^{o}C$. Differences in root:shoot ratios of seedlings at $27^{o}/19^{o}C$, $27^{o}/16^{o}C$ and $27^{o}/10^{o}C$ were not significant.

7.3 THE EFFECTS OF VARIOUS CONSTANT AND AMBIENT SOIL TEMPERATURES

7.3.1 Materials and Methods

Seedlings used in Experiments 4 to 12 of this chapter were raised at the CERES phytotron. Lots of seed were sown at approximately 1½-2 month intervals to ensure a ready supply of seedlings. The seeds (origin: Yarralumla, A.C.T.) were germinated in an open glasshouse maintained at a day/night temperature of $27^{o}/22^{o}C$ (see Chapter 3, Sections 3.2.1 and 3.3.1 for details of the facility and procedures). After transplanting, three to four weeks from sowing, the seedlings were placed in a glasshouse at a day/night temperature of $21^{o}/16^{o}C$ until required for the experiment. Throughout this period seedlings were maintained as described in Chapter 3 (Section 3.3.3).

All lots of seedlings were raised under virtually the same day/night temperature, nutrient and moisture conditions. However, seedlings were subjected to seasonal variations in both photoperiod and radiation. To what extent these seasonal differences affect the subsequent root and shoot growth of root-pruned *P. radiata* is not known. In an attempt to ensure that all seedlings at the time of treatment were conditioned to similar light conditions, the seedlings were acclimatised for three to five weeks in an artificially-lit LBH cabinet (facility detailed in Chapter 3, Section 3.2.1) set at a sixteen hour photoperiod and a light intensity of 630-730 $\mu Em^{-2}sec^{-1}$ (3000-3500 f.c.).

Of the seedlings sown in each lot between sixty and eighty were selected and transferred to the cabinet for acclimation. The day and night air temperature of the cabinet was set to match the air temperature regime at which the seedlings would be grown subsequent to being root-pruned and/or replanted.

The cabinets and apparatus used in controlling constant soil temperatures are detailed in Chapter 3 (Section 3.2.2). In all experiments for both the acclimation and treatment period, the day time air temperatures were maintained for sixteen hours and were synchronized with the sixteen hour light period. The night time air temperatures were held for the remaining eight hours. Light intensities were checked weekly and maintained at 630-730 $\mu Em^{-2}sec^{-1}$.

Eight seedlings were carefully selected for root regeneration potential (RRP) determination for each of the soil temperature treatments.

Another two seedlings per treatment were then selected from the remaining stock. These seedlings were not root-pruned, but planted intact into the various soil temperatures. Because the intact seedlings were chosen from residual stock, they often differed in size from those root-pruned. Root systems of seedlings selected for RRP determination were pruned to 21 cm from the cotyledons and all remaining white root tips were pinched off (detailed in Chapter 3, Section 3.3.4).

Both root-pruned and intact seedlings were replanted into perforated polyethylene bags. The bags allowed for easy placement and removal of the seedlings, into the copper pots secured in the water baths. Special care was taken not to disturb the soil around the roots of intact seedlings when transferring them to the plastic bags.

As the space available at each soil temperature was restricted to only eight pots per water bath, four of the root-pruned seedlings were placed, two per pot. These seedlings were planted into smaller separate plastic bags. Although the soil volume was one half that available to the other seedlings, at no time was there evidence that the soil volume restricted root proliferation. At no time were the soil volumes, even in the smaller bags fully explored by new roots at the end of the three week treatment period. The void spaces between the two bags when placed into the pot of the water bath were packed with moist paper towels. This maintained a constant contact between the soil and pot wall and also prevented air from the cabinet chamber reaching root level and so causing minor temperature variations in the root bags. All seedlings were positioned in the pot so that the shoots did not shade each other.

In some experiments seedlings were kept so that soil temperatures were the same as the ambient day/night air temperature. All of these seedlings were planted into 18 cm pots (of approximate volume as the larger plastic bags). The pots were kept alongside the water baths at the same height as those in the other treatments.

All seedlings were watered with tap water and Hoagland's nutrient solution (Appendix I) that had been adjusted to the soil temperature in which the seedlings were growing. The watering and nutrient schedules varied with the air and soil regimes examined. At the lower air and soil temperatures seedlings were watered every

second day, alternately with water and nutrients. At the higher air temperatures seedlings were watered twice daily, alternately with water and nutrients. Constant checks were made to ensure that the seedlings always had sufficient moisture.

Both root-pruned and intact seedlings were allowed to grow for three weeks under the various soil temperature treatments, then they were harvested. The diameter and height increment, relative growth rate of diameter (RGR_D) and height (RGR_H), final dry weight of the shoot, new root and total root, and root:shoot ratio were determined for each pruned and intact seedling. The RRP of root-pruned seedlings was determined, based on the numbers of new white roots ≥ 0.1 cm (GT), ≥ 1.5 cm (LR), 0.1-1.4 cm (SR) and the total length (TL) and average length (AL) of all new roots produced (GT).

Table 7.7 Various combinations of air and soil temperatures used in Experiments 4 to 13.

Day/ Night Air Temperature (^oC)	Expt. No.	Constant Soil Temperature (^oC)								Soil=Ambient Temperature
		5	10	15	20	25	30	35	40	
15/5	4		*	*						*
	5	*			*					
20/10	6		*	*						*
	7				*	*				
	8				*	*				
25/15	9		*	*	*	*				*
	10				*	*	*	*		
	11				*	*				*
30/20	12			*	*	*	*			*
	13					*	*	*	*	

The numbers of active white root tips were counted on each intact seedling and pinched off for subsequent dry weight determination. The diameters of the three thickest roots per seedling were measured with calipers, two readings per root, and the mean diameter of the three roots recorded as the diameter of active root tips at that soil temperature.

The range of air and soil temperatures selected for the study included temperatures that might be encountered in the nursery or field at different times throughout the year. In some cases the soil temperatures tested were limited by either the availability of the temperature control apparatus or by the capabilities of the apparatus itself. Some soil temperature treatments were replicated two or three times in separate experiments.

The day and night air temperature regimes and the soil temperatures examined at each experiment are outlined in Table 7.7.

The ages of the seedlings, length of acclimation period to which the seedlings were subjected prior to treatment, and the date of treatment are presented in Table 7.8.

Table 7.8 The past history of *P. radiata* seedlings at each experiment.

Experiment Number	Age of Seedlings (days)	Acclimation Period (weeks)	Treatment Date (day/month)
4	122	4	5/5
5	111	4	14/11
6	118	4	12/7
7	130	4	20/10
8	125	4	11/6
9	141	4	27/10
10	108	5	14/12
11	142	4	19/3
12	119	3	12/1
13	155	4	17/2

7.3.2 Statistical Analysis

The data from each experiment were analyzed separately. Because of the variation in the past history of the seedlings and in the times of treatment, it was not possible to analyze all experiments together. Differences between the root-pruned and intact seedlings were not compared.

In experiments with three or more treatments (Experiment 4, 6, 9, 10, 12, 13) the differences between treatment means of each parameter were compared using Duncan's multiple range test at the 5% level. Where only two treatments were examined, comparisons of treatment means were made by t-test. Coefficients of variability were calculated for each parameter measured.

Results of the analyses for both root-pruned and intact seedlings at soil temperatures under the $15^{o}/5^{o}C$, $20^{o}/10^{o}C$, $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ day/night air temperature regimes are presented in Appendix IV, Parts A, B, C and D respectively.

7.3.3 Results

The growth responses of both root-pruned and intact seedlings are discussed separately in this section. The mean value of each root parameter measured for root-pruned seedlings from all the separate experiments are presented together in Tables 7.9 to 7.13 and Figures 7.7 to 7.11. Shoot growth is presented in Tables 7.14 and 7.15. For intact seedlings, root and shoot growth are shown in Tables 7.18 to 7.21. The growth response in each treatment is given in relation to the soil temperature and to the daily heat sum of the soil in degree-hours, calculated as day soil temperature (above ^{o}C) times hours of day soil temperature plus night soil temperature times hours of night soil temperature. As the response of seedlings was closely related to the progressively increasing numbers of soil degree-hours the seedlings received, it was then possible to make growth comparisons between the ambient and constant soil temperatures.

Because the experiments were conducted separately, direct comparisons between some treatments could not be made. Nevertheless, certain inferences can be drawn from the trends of the seedling responses. The erratic results in some treatments, including replicated treatments was most probably due to the previous history of the seedlings examined including preconditioning period, age, initial size or to the environmental factors involved. Even though light

intensity, photoperiod and temperature were controlled other environmental factors such as relative humidity and CO_2 concentration were not. Indeed these factors cannot be replicated exactly in repeated experiments. The differences in root response found suggest the results of any one experiment should not be extrapolated too far.

7.3.3.1 Root-Pruned Seedlings

7.3.3.1.1 Root Regeneration Potential

In the previous series of experiments ambient temperature regimes had a pronounced influence on root regeneration. In this series of experiments where air temperature and soil temperature were separately controlled each was found to exert a separate and significant influence on the root regeneration potential of root-pruned seedlings. The distribution of root growth under the various temperature regimes is presented in the following sections.

a) Total Number of New Roots ≥ 0.1 cm (GT)

Under all air temperatures, there was a tendency for increased root production at the highest soil temperatures (Figure 7.7, Table 7.9). There was a general trend for more roots to be produced at the middle soil temperatures of $15^{o}C$ to $25^{o}C$, but, interestingly the greatest number of new roots (GT) was produced under the coolest air temperature regime of $15^{o}/5^{o}C$ with a constant $15^{o}C$ and a fluctuating $15^{o}/5^{o}C$ soil temperature. Significantly more roots were produced at the ambient soil temperature than the $10^{o}C$ soil temperature, but a further rise in soil temperature to $15^{o}C$ resulted in a small but insignificant increase. The numbers of roots produced at the $20^{o}C$ soil temperature was considerably lower than at $10^{o}C$ or $15^{o}C$ but this could have been the result of differences between seedlings in the experiments (see Appendix IV.A.1).

The total numbers of new roots produced under the $20^{o}/10^{o}C$ air temperature regime were much lower than under any of the other temperature regimes tested, for the same soil temperatures. However, the same trends were apparent, the numbers of roots produced steadily increased with increases in soil temperature.

Under the $25^{o}/15^{o}C$ air temperature high numbers of roots were produced and once again the numbers of new roots produced

Table 7.9 Effect of soil temperature at different day/night air temperatures on the total number of new roots ≥0.1 cm (GT) produced by root-pruned seedlings in 3 weeks. Values are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	55			
10	240	80	4	36	
15/5	280	238			
15	360	261	47	110	159
20/10	400		68		
20	480	149	123,6	208,205, 44	234
25/15	520			211,136	
25	600		172,53	206,155, 87	171,130
30/20	640				197
30	720			161	217,169
35	840			11	29
40	960				0

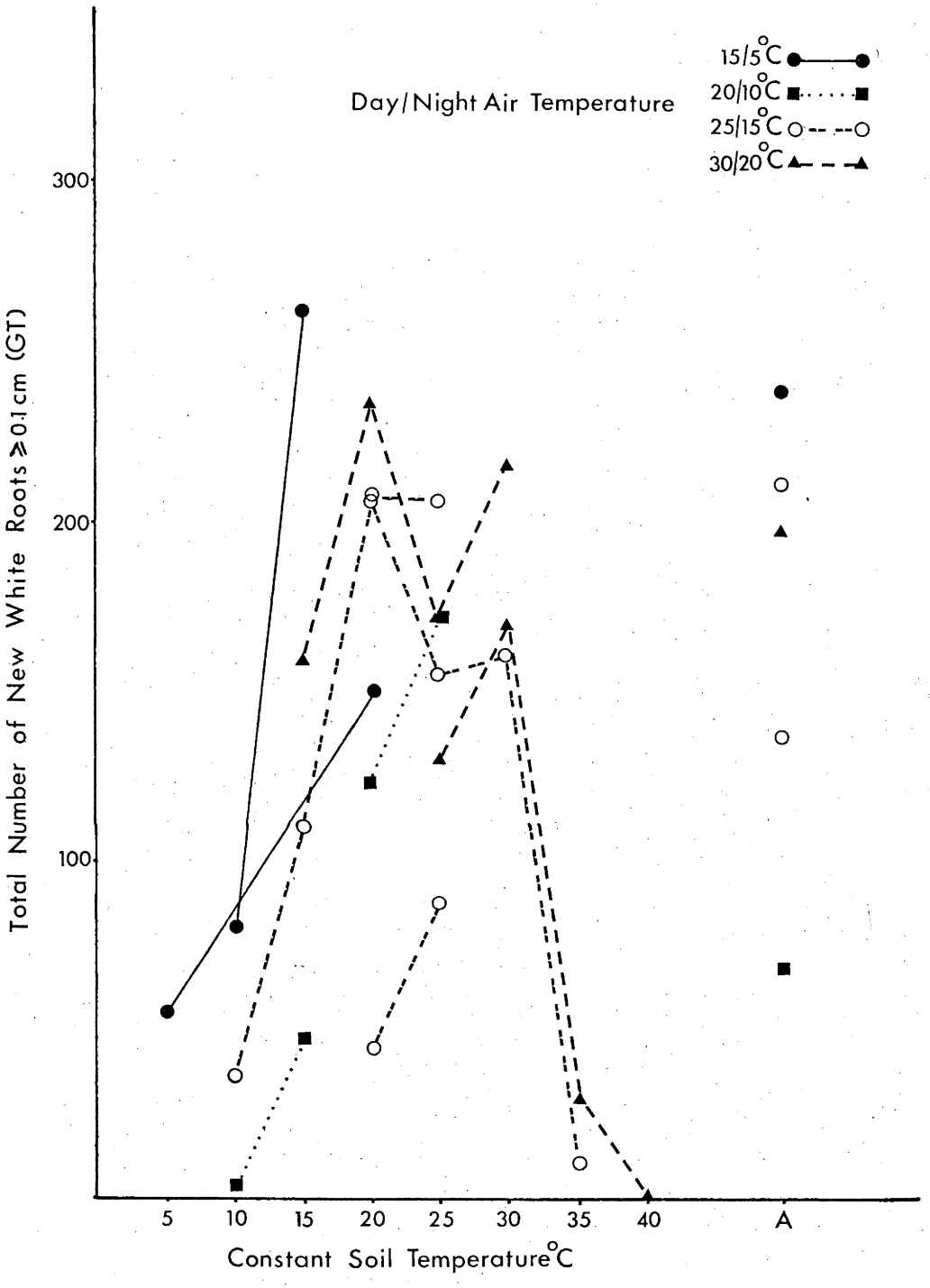

Figure 7.7. The total number of new white roots ≥ 0.1 cm (GT) produced by seedlings at various air and soil temperatures three weeks after root-pruning. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

increased with increasing soil temperature. The highest numbers were attained at soil temperatures from 20°C to 30°C. Although the root numbers in the replicated treatments at 20°C, 25°C and at the ambient 25°/15°C varied, the general response to temperature was similar. Increases in soil beyond 25°C reduced the numbers of root produced, only slightly at 30°C but most significantly at 35°C.

Under the 30°/20°C air temperature increases in soil temperature from 15°C to 30°C had no marked effect on the numbers of new roots produced, root production was similar at all soil temperatures tested within this range. Soil temperatures beyond 30°C, however, drastically reduced the numbers of root produced. At a soil temperature of 40°C no root growth was observed and by the end of the experiment two of the eight seedlings were dead. With minor exceptions, the numbers of roots produced under the 30°/20°C and 25°/15°C air temperature regimes were quite comparable at the respective soil temperatures.

Soil temperature had a marked effect on the morphology of the new roots produced under all the air temperature regimes. The most striking differences were observed between new roots at the lowest air and soil temperatures and those under the higher air and soil temperatures.

Low temperatures stimulated the production of thick, white, succulent roots. The roots were also very brittle as they could easily be snapped in half and no lateral root initiation was observed along the new roots. At the higher temperatures the new roots were thinner, tan to brown in colour and more flexible. Initiation of lateral roots along the new roots was greatest at these temperatures and as indicated by the larger proportion of brown to white new root, the rate of suberization was faster.

b) Number of New Roots 0.1-1.4 cm (SR)

As shown in Tables 7.9 and 7.10, short roots (SR) made up a considerable proportion of the total new roots produced. The significant increase in the number of SR at the highest soil temperatures under the 15°/5°C regime alone accounts for the large total number of root (GT) scored under this cool air temperature. At soil temperatures of 10°C to 15°C more SR were produced under the 15°/5°C regime than at any other temperature (Figure 7.8).

Table 7.10 Effect of soil temperature at different day/night air temperatures on the number of new roots 0.1-1.4 cm (SR) produced by root-pruned seedlings in 3 weeks. Values are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	51			
10	240	75	4	35	
15/5	280	180			
15	360	184	32	105	121
20/10	400		44		
20	480	70	41,6	142,178,38	124
25/15	520			124,108	
25	600		64,48	122,91,56	77,94
30/20	640				93
30	720			135	103,132
35	840			11	26
40	960				0

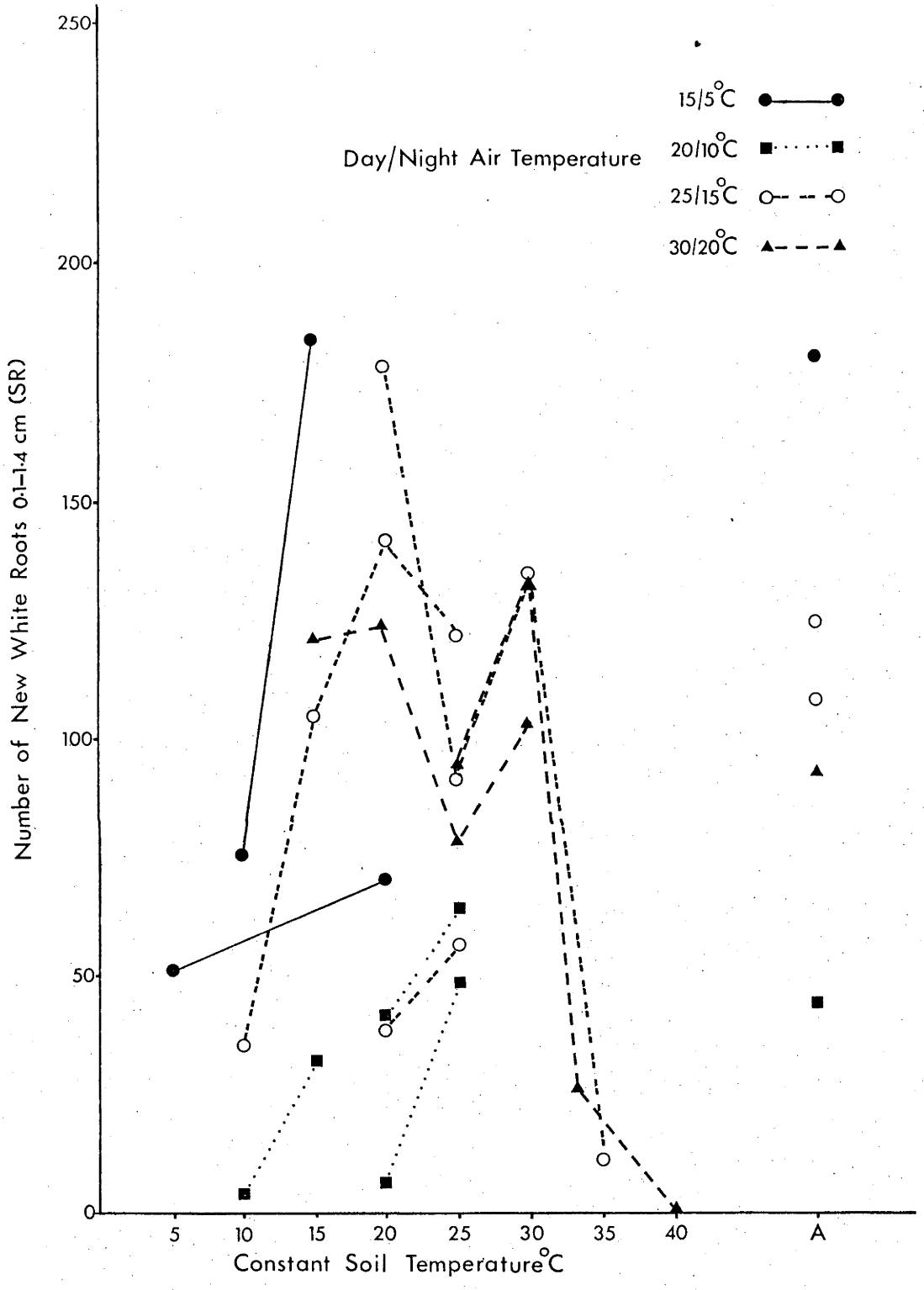

Figure 7.8. The number of new white roots 0.1-1.4 cm (SR) produced by seedlings at various air and soil temperatures three weeks after root-pruning. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

Under the 25°/15°C air temperature, the significant proliferation of SR occurred at soil temperatures of 15°C to 30°C, with the highest numbers of SR at the 20°C soil temperature. Experiment 10 was the exception, with the greatest numbers of SR at the ambient 25°/15°C soil temperature. At a soil temperature of 30°C approximately 83 per centof the new roots produced (GT) were short roots and at 35°C root growth was stricted to a few short roots only.

Increases in soil temperature from 15°C to 30°C under the 30°/20°C air temperature also had little effect on the numbers of SR produced. Increases in soil temperature above 30°C drastically reduced the numbers of SR. Short root numbers under the 25°/15°C and 30°/20°C air temperatures were comparable.

Some mychorrizal activity was evident under all air temperature regimes. Generally, the soil temperatures which favoured root growth favoured growth of mychorrizal roots. Most of the mychorrizal roots observed were typically dichotomously branched (Cromer, 1935), few formed corraloid clusters. A number of mychorrizal roots were scored as short roots (SR) at soil temperatures above 10°C under the 25°/15°C and 30°/20°C air temperature regimes, however, the greatest portion of SR was made up of short lateral roots initiated along the long new roots at these temperatures.

c) Number of New Roots ≥ 1.5 cm (LR)

The numbers of long roots (LR) produced by seedlings was markedly influenced by air and soil temperature (Table 7.11, Figure 7.9). In most treatments, the number of SR exceeded the number of LR produced. Under the 15°/5°C air temperature, this proportion of LR to SR increased with increasing soil temperature. At a soil temperature of 20°C over half the roots were LR indicating that warm soil temperatures under the cool air temperatures favour more rapid growth of new roots formed and hence resulted in a higher score for LR.

Increasing the air temperature to 20°/10°C had little effect on LR produced. The numbers of LR increased with increasing soil temperature but the increases were not significant. The greater numbers of LR than SR at soil temperatures of 20°C and 25°C (Experiment 6) agree with the greater numbers of LR than SR at a 20°C soil temperature under the 15°/5°C air temperature and at soil temperatures of 30°/20°C and 30°C under the 30°/20°C air temperature. All

Table 7.11 Effect of soil temperature at different day/night air temperatures on the number of new roots ≥1.5 cm (LR) produced by root-pruned seedlings in 3 weeks. Values are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	4			
10	240	5	1	1	
15/5	280	58			
15	360	77	15	5	38
20/10	400		24		
20	480	79	82,2	66,27,6	110
25/15	520			87,35	
25	600		108,5	84,64,31	94,36
30/20	640				104
30	720			26	114,37
35	840			0	3
40	960				0

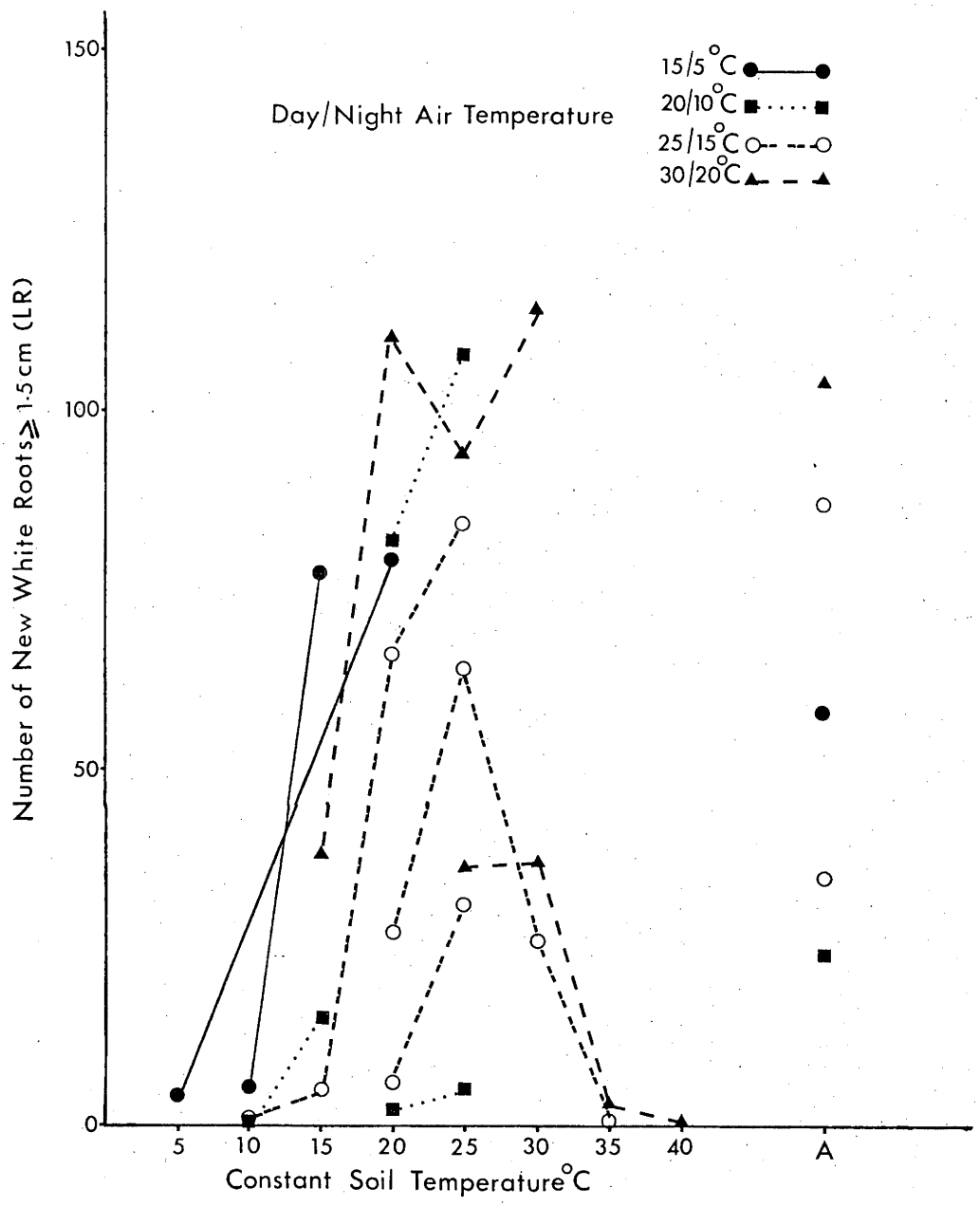

Figure 7.9. The number of new white roots ≥ 1.5 cm (LR) produced by seedlings at various air and soil temperatures three weeks after root-pruning. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

of these soil temperatures favoured LR growth. They lie within a range of soil daily heat sum between 480 and 720 degree-hours.

Soil temperatures under the $25^{o}/15^{o}C$ air temperature had a marked influence on the numbers of LR produced. Cool soil temperatures of $10^{o}C$, $15^{o}C$ and to a less extent even $20^{o}C$ resulted in reduced LR. The low number of LR at $10^{o}C$ was comparable to the numbers of LR at both $15^{o}/5^{o}C$ and $20^{o}/10^{o}C$ air temperatures. The highest numbers of LR were attained at soil temperatures of $25^{o}C$ and $25^{o}/15^{o}C$. Soil temperatures above or below these, resulted in marked reductions in numbers of LR. At a soil temperature of $35^{o}C$ no LR were produced.

Under the $30^{o}/20^{o}C$ temperature regime cooler soils of $15^{o}C$ resulted in reduced numbers of LR, however, statistically only LR at $30^{o}C$ and this temperature were significantly different. Relatively little difference was found in LR produced at soils from $20^{o}C$ to $30^{o}C$. Large numbers of LR were produced at these soil temperatures. Increasing soil temperature to $35^{o}C$ reduced the numbers of LR considerably. Root growth at this temperature was restricted to the proliferation of only a few short roots (SR) in most seedlings. Statistically, however, the numbers of LR at soil temperatures of $35^{o}C$ and $40^{o}C$ were not significantly different to those at soil temperatures of $25^{o}C$ and $30^{o}C$.

The SR and LR recorded for the $35^{o}C$ soil treatment were produced by only three seedlings. Interestingly, the LR produced by these seedlings developed at the uppermost part of the root sytem and were lying almost at the surface of the planting medium. Production of roots so close to the air/soil interface might suggest there was a temperature gradient between the soil and air and the very upper layer of soil was a little cooler than $35^{o}C$.

d) Total Length of New Roots $\geq$ 0.1 cm (TL)

The various air and soil temperature combinations had marked effects on the total length of new roots produced (Table 7.12, Figure 7.10). In general, temperatures which favoured production of great numbers of roots especially LR, produced the greatest length of roots (TL).

Under the coolest air temperature ($15^{o}/5^{o}C$) the total length of new roots increased with increasing soil temperature. Seedlings at

Table 7.12 Effect of soil temperature at different day/night air temperatures on the total length of new roots (TL) produced by root-pruned seedlings in 3 weeks. The values in cm are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	404			
10	240	48.1	2.3	16.2	
15/5	280	248.8			
15	360	303.6	60.6	58.5	164.4
20/10	400		99.4		
20	480	323.8	394.3,3.5	243.3,171.2, 35.0	433.2
25/15	520			382.8,148.8	
25	600		516.8,43.6	420.1,264.9, 121.8	395.2, 181.3
30/20	640				452.7
30	720			154.7	597.2, 150.9
35	840			3.2	18.8
40	960				0.0

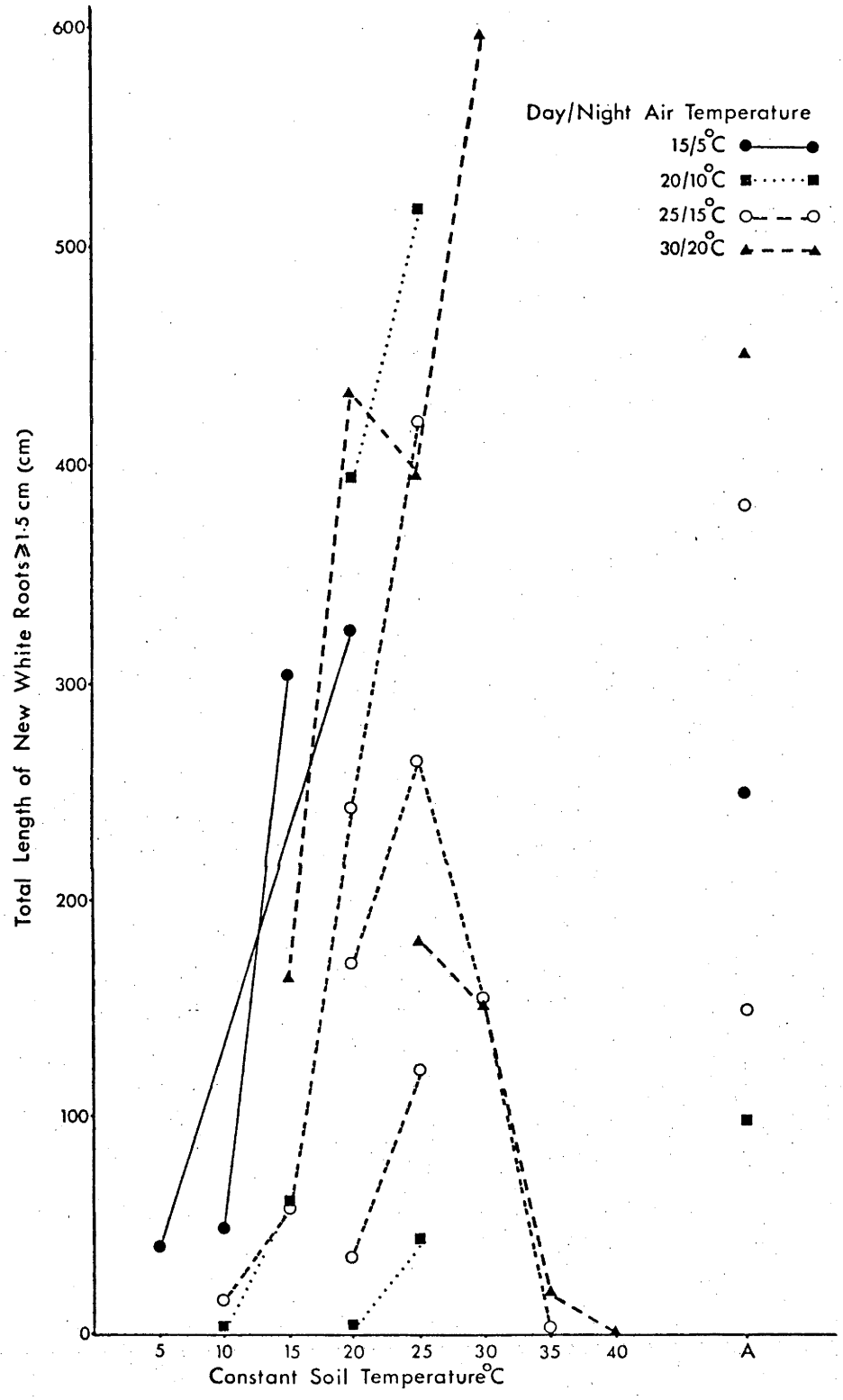

Figure 7.10. The total length of new white roots ≥ 0.1 cm (TL) produced by seedlings at various air and soil temperatures three weeks after root-pruning. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

the warmer soil temperatures produced significantly longer lengths of new root than at the cooler soil temperatures examined.

The same trend was shown by seedlings under the $20^{o}/10^{o}C$ air temperature regime. Despite some variability in the replicated treatments at soil temperatures of $20^{o}C$ and $25^{o}C$, results indicate that the TL at soil temperatures of $20^{o}C$ and $25^{o}C$ was greater than at $10^{o}C$. Increasing the day/night air temperature from $20^{o}/10^{o}C$ to $25^{o}/15^{o}C$ made little difference to TL at the coolest soil temperature. Cool soil temperatures resulted in significantly lower TL than at soil temperatures of $25^{o}/15^{o}C$ and $25^{o}C$, which produced the greater lengths of new root. Within a range of soil temperatures from $20^{o}C$ to $30^{o}C$ substantial lengths of root were produced, but there was a sharp decline in length of root produced at soil temperatures in excess of $30^{o}C$.

Under air temperatures of $30^{o}/20^{o}C$, soil temperatures from $20^{o}C$ to $30^{o}C$ were once again most beneficial for the extension of roots. As soil temperature was reduced below $20^{o}C$ to $15^{o}C$ TL decreased substantially, however, statistically the differences were not significant. With minor variations the TL of new roots under the $30^{o}/20^{o}C$ and $25^{o}/15^{o}C$ air temperatures were comparable. At both air temperatures increases in soil temperature above $30^{o}C$ resulted in drastic reductions in TL.

e) Average Length of New Roots ≥ 0.1 cm (AL)

The average lengths of all the new roots produced by seedlings under the various soil and air temperature regimes are presented in Table 7.13 and Figure 7.11. Soil temperature had a strong influence on the average length (AL) of the new roots. Under the coolest air temperature regime root lengths (AL) tended to increase with increases in soil temperature. The longest roots were produced at soil temperatures of $15^{o}/5^{o}C$ and greater.

Under the $20^{o}/10^{o}C$ air temperature there were only slight increases in AL with increasing soil temperature. Warm soils, however, were most favourable.

New roots produced under the $25^{o}/15^{o}C$ air temperature were on the average longer at soil temperatures of $25^{o}C$ and $25^{o}/15^{o}C$. Soil temperatures above or below these reduced AL considerably. The

Table 7.13 Effect of soil temperature at different day/night air temperatures on the average length of new roots (AL) produced by root-pruned seedlings in 3 weeks. The values in cm are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.73			
10	240	0.58	0.64	0.52	
15/5	280	0.99			
15	360	1.08	1.01	0.52	1.01
20/10	400		1.17		
20	480	2.08	3.07,0.58	1.10,0.86, 0.72	1.79
25/15	520			1.55,1.06	
25	600		3.05,0.79	2.02,1.73, 1.38	2.27,1.25
30/20	640				2.22
30	720			0.96	2.51,0.70
35	840			0.28	0.41
40	960				0.00

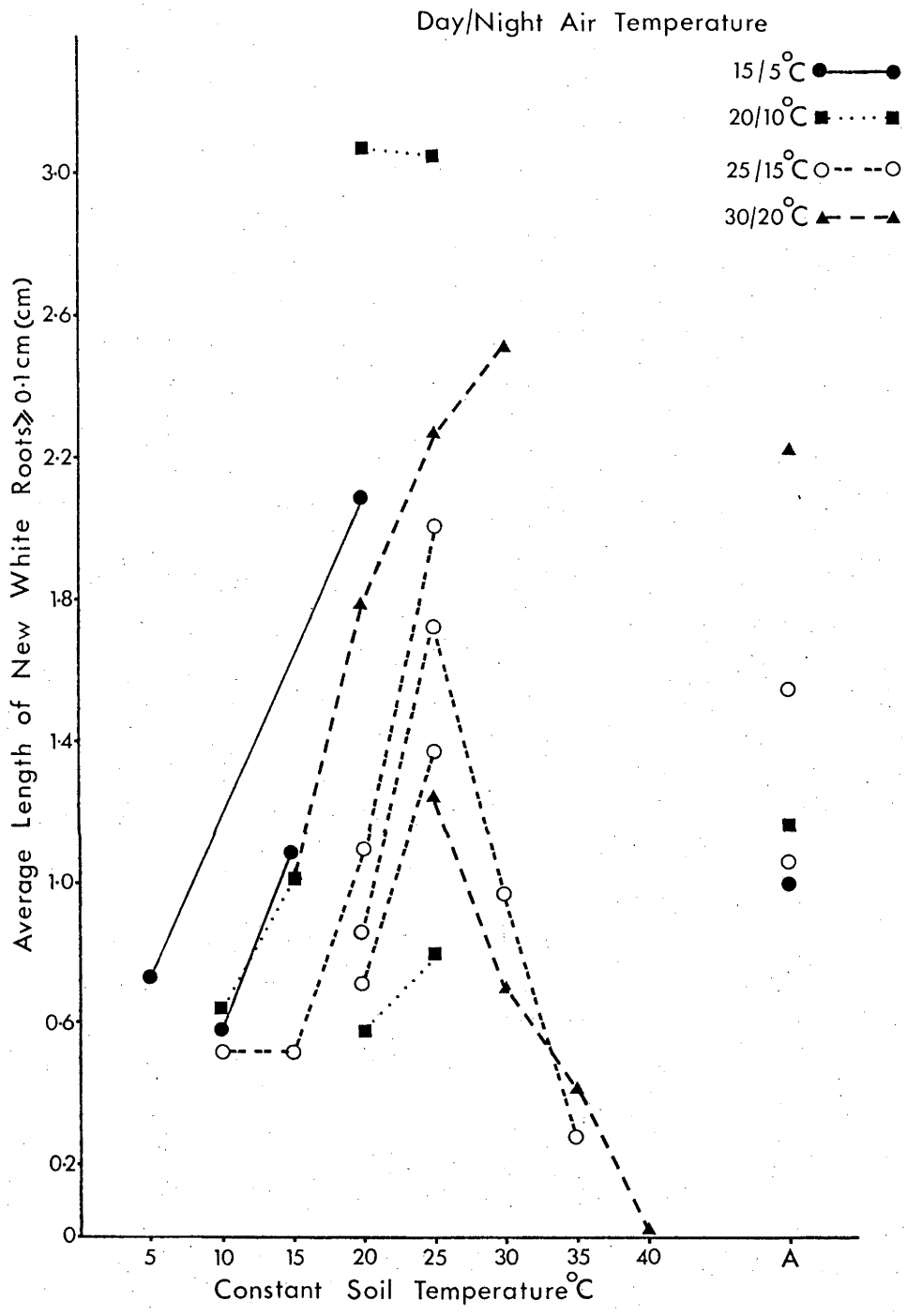

Figure 7.11. The average length of new white roots ≥ 0.1 cm (AL) produced by seedlings at various air and soil temperatures three weeks after root-pruning. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

AL of new roots at soil temperatures of $20^{o}C$ and $30^{o}C$ were not different.

Under the $30^{o}/20^{o}C$ air temperature soil temperatures from $20^{o}C$ to $30^{o}C$ produced the higher AL of new roots. Soil temperatures below $20^{o}C$ and above $30^{o}C$ reduced AL.

7.3.3.1.2 Shoot Growth

a) Diameter

With the exception of seedlings in Experiment 6, diameter increment and the relative rate of diameter growth (RGR_D) was greatest at the lowest air temperature regime, especially under the warmer soil temperatures (Table 7.14). Statistically there were no differences in diameter growth (diameter increment and RGR_D) between the soil temperatures examined at this air temperature.

Under the $20^{o}/10^{o}C$ air temperature regime diameter growth increased with increasing soil temperature. Differences in diameter growth between a soil temperature of $10^{o}C$ and $20^{o}/10^{o}C$ soil temperature were significant. Increasing soil temperatures from $20^{o}C$ to $25^{o}C$ had little effect on diameter growth.

Soil temperatures under the $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures also had little effect on diameter growth. Increasing the soil temperature to $40^{o}C$ at an air temperature of $30^{o}/20^{o}C$ did however have a marked adverse effect on diameter growth.

b) Height

Both air and soil temperature had a significant effect on height growth of seedlings. Height growth (height increment and RGR_H) was equally poor for seedlings under the coolest air temperature regime at all soil temperatures, and at the highest soil temperatures under the highest air temperatures (Table 7.15).

Soil temperatures under the $15^{o}/5^{o}C$ air temperature regime had no significant effect on height growth. Seedlings at all soil temperatures responded similarly. Increasing the air temperature above $15^{o}/5^{o}C$ resulted in marked increases in height growth but increases in soil temperature above $10^{o}C$ under the warmer air temperature regimes had little effect on height growth. A soil temperature of $40^{o}C$ sharply reduced height growth.

Table 7.14 Effect of soil temperature at different day/night air temperatures on the diameter growth of seedlings 3 weeks after root-pruning. Values are the means of 8 replicates.

A Diameter Increment (mm)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	0.78			
10	240	0.76	0.44	0.32	
15/5	280	0.75			
15	360	0.86	0.62	0.29	0.26
20/10	400		0.75		
20	480	0.96	1.36,0.23	0.38,0.36, 0.05	0.25
25/15	520			0.30,0.20	
25	600		1.29,0.29	0.41,0.28, 0.25	0.39,0.29
30/20	640				0.39
30	720			0.44	0.48,0.38
35	840			0.38	0.60
40	960				0.17

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Table 7.14 (Cont'd)

B Relative Rates of Diameter Growth
(mm/mm/day)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.0057			
10	240	0.0081	0.0048	0.0031	
15/5	280	0.0079			
15	360	0.0094	0.0068	0.0030	0.0031
20/10	400		0.0075		
20	480	0.0068	0.0136, 0.0021	0.0040, 0.0036, 0.0016	0.0030
25/15	520			0.0032, 0.0019	
25	600		0.0141, 0.0026	0.0042, 0.0031, 0.0022	0.0048, 0.0031
30/20	640				0.0047
30	720			0.0045	0.0059, 0.0040
35	840			0.0040	0.0061
40	960				0.0017

Table 7.15 Effect of soil temperature at different day/night air temperatures on the height growth of seedlings 3 weeks after root-pruning. Values are the means of 8 replicates.

A Height Increment (cm)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.80			
10	240	0.69	1.84	1.94	
15/5	280	0.59			
15	360	0.70	1.54	1.92	1.42
20/10	400		1.60		
20	480	0.94	2.16,1.27	2.04,1.04, 0.26	2.20
25/15	520			1.71,0.73	
25	600		2.28,1.00	1.92,0.98, 0.60	1.10,1.01
30/20	640				1.71
30	720			1.12	1.88,1.72
35	840			0.74	1.85
40	960				0.56

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Table 7.15 (Cont'd)

B Relative Rates of Height Growth (cm/cm/day)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	0.0014			
10	240	0.0017	0.0047	0.0040	
15/5	280	0.0015			
15	360	0.0017	0.0041	0.0041	0.0048
20/10	400		0.0041		
20	480	0.0017	0.0141, 0.0025	0.0043, 0.0027, 0.0004	0.0067
25/15	520			0.0036, 0.0016	
25	600		0.0115, 0.0023	0.0041, 0.0025, 0.0014	0.0034, 0.0025
30/20	640				0.0054
30	720			0.0030	0.0060, 0.0041
35	840			0.0019	0.0046
40	960				0.0014

7.3.3.1.3 Final Dry Weight

a) Shoot, Regenerated Root and Total Root Dry Weight

As shown in Appendix IV the shoot and total root dry weight of seedlings did not differ significantly between treatments in most experiments. The only exceptions were under the $15^{o}/5^{o}C$ (Experiment 4) and $25^{o}/15^{o}C$ (Experiment 8) air temperature regimes.

Under the $15^{o}/5^{o}C$ air temperature total root dry weight was significantly greater at the $20^{o}C$ soil temperature than at the $5^{o}C$ soil temperature. Similarly seedlings under the $25^{o}/15^{o}C$ air temperature at the warmer soil temperatures of $25^{o}C$ and $25^{o}/15^{o}C$ produced the heavier total root dry weights compared to seedlings at cool soil temperatures of $10^{o}C$ and $15^{o}C$.

Shoot dry weights generally corresponded closely with the height and diameter growth of the seedlings under the various temperature treatments. Final total root dry weights reflected the root growth at the various temperatures.

The regenerated root dry weights of seedlings in all treatments (Table 7.16) were closely related to the total lengths and numbers of new root produced. In general, the greater dry weights were found at the warmer soil temperature treatments under each air temperature regime.

b) Root:Shoot Ratio

With few exceptions, the root:shoot ratios of seedlings differed little between soil temperature treatments in each experiment at the end of the three week treatment period (Table 7.17). Under the highest air temperatures root:shoot ratios were comparable. However, root:shoot ratios of seedlings at the $25^{o}C$ soil temperature under the $30^{o}/20^{o}C$ air temperature were significantly higher than those at $15^{o}C$ and $20^{o}C$ soils. These cooler soils made no difference to root:shoot ratios of seedlings under the $25^{o}/15^{o}C$ air temperature.

Seedlings under the $15^{o}/5^{o}C$ air temperature regime tended to have the greatest root:shoot ratios of all treatments. At soil temperatures of $10^{o}C$ to $15^{o}C$ root:shoot ratios were higher under the $15^{o}/5^{o}C$ air temperature than under the warmer air temperatures.

Table 7.16 The regenerated root dry weights of seedlings under various air and soil temperature regimes. The values in grams are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	0.020			
10	240	0.034	0.001	0.017	
15/5	280	0.112			
15	360	0.138	0.022	0.018	0.054
20/10	400		0.063		
20	480	0.264	0.350,0.002	0.085,0.048, 0.009	0.122
25/15	520			0.162,0.037	
25	600		0.308,0.021	0.144,0.081, 0.054	0.132, 0.064
30/20	640				0.160
30	720			0.049	0.202, 0.053
35	840			0.008	0.007
40	960				0.000

Table 7.17 Effect of soil temperature at different day/night air temperatures on the root:shoot ratio (by dry weight) of seedlings 3 weeks after root-pruning. Values are the means of 8 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	0.27			
10	240	0.39	0.22	0.25	
15/5	280	0.36			
15	360	0.41	0.26	0.26	0.29
20/10	400		0.23		
20	480	0.34	0.43,0.28	0.25,0.31, 0.28	0.28
25/15	520			0.28,0.30	
25	600		0.48,0.24	0.28,0.30, 0.29	0.35,0.30
30/20	640				0.30
30	720			0.30	0.30,0.26
35	840			0.31	0.26
40	960				0.25

7.3.3.2 Intact Seedlings

7.3.3.2.1 Root Growth

a) Number of Active White Roots

Results presented in Table 7.18 indicate that active root growth of intact seedlings is favoured over a much wider range of soil temperatures than is root growth of root-pruned seedlings. The most apparent similarities in growth patterns are the large numbers of active white roots at the lower air temperatures and the restricted root growth at the higher soil temperatures.

Under the $15^{o}/5^{o}C$ air temperature large numbers of active root tips were found on intact seedlings at all soil temperatures except $20^{o}C$. The smaller numbers produced at this soil temperature suggests this temperature may stimulate more rapid suberization of roots and therefore, less white root tips, yet on the other hand, may indicate reduced active root growth when soil temperatures exceed the ambient temperatures for the shoot.

Soil temperature had little effect on the numbers of active roots scored under the $20^{o}/10^{o}C$, $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures. There was a slight tendency for greater numbers to be found on seedlings at the warmer soil temperatures. Although not significantly different from the other treatments, at $35^{o}C$ soil temperatures there was a slight reduction in numbers of active root tips indicative of the greater suberization of roots at this temperature and restriction of both root and mycorrhizal growth. The active white tips removed were short, with the remaining root system heavily suberized. Seedlings at the highest soil temperature of $40^{o}C$ under the $30^{o}/20^{o}C$ air temperature possessed no active roots. The root systems were fully suberized.

b) Diameter of Active White Roots

As shown in Table 7.19 thicker root tips were produced at all the soil temperatures under the lowest air temperature regime and under the coolest soil temperatures of the $20^{o}/10^{o}C$, $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures. In general, the higher air and soil temperatures produced the finer (thinner) roots. Under both the $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperature regimes increases in soil temperature

Table 7.18 The numbers of active white root tips found on intact seedlings at various air and soil temperatures. Values are the means of 2 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	386			
10	240	566	179	443	
15/5	280	561			
15	360	446	221	449	283
20/10	400		214		
20	480	92	276,218	510,310, 132	98
25/15	520			596,200	
25	600		235,30	403,168, 80	215,14
30/20	640				196
30	720			292	337,202
35	840			58	51
40	960				0

Table 7.19 Diameters of the active white root tips found on intact seedlings at various air and soil temperatures. The values in mm are the means of 6 root measurements.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	1.54			
10	240	2.44	2.16	2.17	
15/5	280	2.28			
15	360	2.24	1.77	2.04	1.52
20/10	400		2.10		
20	480	2.12	1.82,1.68	1.84,1.52, 1.76	1.20
25/15	520			1.66,1.36	
25	600		1.52,1.48	1.38,1.12, 1.68	1.24,1.50
30/20	640				1.42
30	720			1.75	1.24,1.65
35	840			1.41	1.19
40	960				-

from 15°C to 20°C made little difference to the thickness of new roots. Root diameters were comparable at the warmer air temperatures.

7.3.3.2.2 Shoot Growth

a) Diameter

As shown by Tables 7.14 and 7.20 diameter growth of intact seedlings was greater than that of pruned seedlings at all soil temperatures. The growth patterns of the intact seedlings differed slightly in response to different soil temperatures.

Under the 15°/5°C temperature regime soil temperature had no significant effect on diameter growth, but, there was a tendency for poor diameter growth at soil temperatures higher than ambient air temperature.

Increasing the air temperature from 15°/5°C to 20°/10°C increased diameter growth of seedlings under most soil temperatures. Soil temperature had no significant effect on diameter growth under the 20°/10°C air temperature.

At a higher air temperature of 25°/15°C, soil temperatures of 10°C to 30°C made little difference to diameter growth. Diameter growth at soil temperatures of 10°C and 15°C was comparable to that at the lower 20°/10°C and 15°/5°C air temperatures.

Increasing the soil temperature to 35°C increased diameter growth to the highest value recorded for this air temperature regime, much as for Experiment 4 in the 20°/10°C set of results and at the warmest soil temperature at 30°/20°C air temperature.

Soil temperatures above 25°C under the 30°/20°C air temperature were most favourable for diameter growth, whereas, soil temperatures below 25°C resulted in marked reductions in diameter growth. Seedlings under the 30°/20°C air temperature were more sensitive to cooler soil temperatures than seedlings at 25°/15°C, otherwise growth at the other soil temperatures was comparable.

b) Height Growth

Height growth of intact seedlings, as might be expected, was greater than that of root-pruned seedlings at most soil temperatures (Table 7.15 and 7.21). The general growth pattern of intact and root-pruned seedlings differed slightly.

Table 7.20 Diameter growth of intact seedlings after 3 weeks under various air and soil temperature regimes. Values are the means of 2 replicates.

A Diameter Increment (mm)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	1.26			
10	240	1.39	1.49	1.27	
15/5	280	1.68			
15	360	1.41	1.33	1.40	0.60
20/10	400		1.68		
20	480	0.84	1.56,1.00	1.48,1.07, 0.74	0.53
25/15	520			1.44,0.88	
25	600		1.96,0.58	1.26,0.88, 0.86	0.84,0.42
30/20	640				0.98
30	720			0.86	1.18,0.89
35	840			1.94	1.37
40	960				1.58

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Table 7.20 (Cont'd)

B Relative Rates of Diameter Growth
(mm/mm/day

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.0108			
10	240	0.0120	0.0156	0.0121	
15/5	280	0.0144			
15	360	0.0125	0.0146	0.0132	0.0083
20/10	400		0.0162		
20	480	0.0075	0.0148, 0.0078	0.0133, 0.0095, 0.0074	0.0075
25/15	520			0.0135, 0.0080	
25	600		0.0176, 0.0047	0.0120, 0.0079, 0.0075	0.0114, 0.0046
30/20	640				0.0124
30	720			0.0085	0.0153, 0.0105
35	840			0.0169	0.0151
40	960				0.0170

Table 7.21 Height growth of intact seedlings after 3 weeks under various air and soil temperature regimes. Values are the means of 2 replicates.

A. Height Increment

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.90			
10	240	1.80	3.33	3.25	
15/5	280	1.95			
15	360	1.80	2.93	3.15	2.40
20/10	400		2.85		
20	480	0.60	4.80,2.45	2.20,2.50, 1.25	1.40
25/15	520			435,1.20	
25	600		3.97,1.90	2.70,1.95, 1.00	1.95,1.40
30/20	640				3.35
30	720			1.70	2.95,2.35
35	840			3.40	2.60
40	960				2.40

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Table 7.21 (Cont'd)

B Relative Rates of Height Growth (cm/cm/day)

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.0021			
10	240	0.0040	0.0080	0.0069	
15/5	280	0.0037			
15	360	0.0044	0.0083	0.0065	0.0094
20/10	400		0.0083		
20	480	0.0017	0.0169, 0.0043	0.0046, 0.0047, 0.0029	0.0061
25/15	520			0.0086, 0.0034	
25	600		0.0144, 0.0036	0.0052, 0.0043, 0.0026	0.0079, 0.0042
30/20	640				0.0132
30	720			0.0037	0.0115, 0.0075
35	840			0.0067	0.0074
40	960				0.0065

Seedlings under the influence of a cool air temperature were growing at a considerably slower rate (RGR_H) than seedlings at the same soil temperatures under warmer air temperatures. Height growth did not differ between the treatments examined under the $15^{o}/5^{o}C$ air temperature regime. However, reduced height growth at a soil temperature of $20^{o}C$ suggests once again some slackening of growth when soil temperatures exceed the ambient air temperature.

Under the $20^{o}/10^{o}C$ air temperature no differences in height growth were found between the higher and lower soil temperatures. At all soil temperatures height growth was greater than under the $15^{o}/5^{o}C$ regime, indicating the favourable influence of an increased air temperature. Soil temperature also had little influence on height growth at the $25^{o}/15^{o}C$ temperature regime.

The higher soil temperatures from $25^{o}C$ to $35^{o}C$ under both the $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures did not reduce height growth. Under the $25^{o}/15^{o}C$ air temperature height growth was enhanced by increasing the soil temperatures from $30^{o}C$ to $35^{o}C$. Similarly, under the $30^{o}/20^{o}C$ air temperature, soil temperatures at and above $30^{o}C$ were favourable. Even at soil temperatures of $40^{o}C$ height growth was surprisingly high, despite the absence of active white roots noted earlier.

7.3.3.2.2 Final Dry Weight

a) Shoot, New Root and Total Root Dry Weight

With one exception, the shoot and total root dry weights of the intact seedlings did not differ statistically between treatments in all experiments (see Appendix IV). The exception was the significantly greater shoot weight of seedlings at the $20^{o}C$ soil temperature than the $5^{o}C$ soil temperature under the $15^{o}/5^{o}C$ air temperature regime (Experiment 4). From the initial height and diameter measurements for these seedlings in Appendix IV.A.1, it appears that initial size rather than the treatment would account for the differences in dry weight.

As shown in Tables 7.18, 7.19 and 7.22 the dry weights of the active white roots of the intact seedlings is closely related to the numbers and diameters (thickness) of the active roots. In this regard, seedlings at soil temperatures under the coolest air temperature regime and cooler soils of the warmer air temperature regimes had the

Table 7.22 The dry weights of the active white root tips found on intact seedlings under various air and soil temperature regimes. The values in grams are the means of 2 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.380			
10	240	0.622	0.589	0.430	
15 /5	280	0.944			
15	360	0.500	0.510	0.700	0.515
20 /10	400		0.595		
20	480	0.172	0.473,0.379	0.459,0.535, 0.191	0.229
25/15	520			0.692,0.135	
25	600		0.279,0.062	0.330,0.156, 0.153	0.135, 0.014
30 /20	640				0.234
30	720			0.356	0.190, 0.191
35	840			0.049	0.038
40	960				0.00

heaviest new root dry weights. Just as the actual root counts varied between treatments, so did the dry weights. Only differences between treatments in Experiment 11, were significant.

b) Root:Shoot Ratio

Root:shoot ratios of intact seedlings were greater than that of root-pruned seedlings in all but the highest soil temperatures under the warmer air temperatures, where root:shoot ratios were comparable (Tables 7.13 and 7.23).

At the soil temperatures examined, seedlings under the $15^{o}/5^{o}C$ air temperature had the highest root:shoot ratios. Under this cooler air temperature there was a tendency for larger root:shoot ratios with increasing soil temperature. Differences between the highest and lowest soil temperature in each experiment were significant. Increases in soil temperature under the $20^{o}/10^{o}C$ air temperature regime made little difference to seedling root:shoot ratios. Differences between treatments in all experiments were not significant.

Under a $25^{o}/15^{o}C$ air temperature, soil temperature had a significant influence on seedling root:shoot ratios. A cool soil temperature of $10^{o}C$ reduced the ratios significantly, whereas, increases in soil temperature from $15^{o}C$ to $25^{o}C$ made little difference to the value of the ratio. Root:shoot ratios were highest at the $25^{o}C$ soil temperature, but only slightly reduced at $35^{o}C$.

The root:shoot ratios of seedlings under the highest air temperature were less sensitive to cool soil temperature than seedlings under the $25^{o}/15^{o}C$ air temperature. Decreases in soil temperature from $30^{o}/20^{o}C$ to $15^{o}C$ did not change the values. Increasing the soil temperature to $30^{o}C$, however, resulted in much lower root:shoot ratios, but only significantly different from the ratios at the $20^{o}C$ soil temperature. Further increases in soil temperature from $30^{o}C$ to $40^{o}C$ significantly reduced the ratios.

The root:shoot ratios under the $25^{o}/15^{o}C$ and to a certain extent $20^{o}/10^{o}C$ air temperatures were comparable at all soil temperatures examined. At the highest soil temperatures of the $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ temperature regime root:shoot ratios were identical.

Table 7.23 Root:shoot ratios (by dry weight) of intact seedlings after 3 weeks under various air and soil temperature regimes. Values are the means of 2 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	0.50			
10	240	0.49	0.42	0.40	
15/5	280	0.60			
15	360	0.74	0.49	0.56	0.63
20/10	400		0.49		
20	480	0.78	0.53,0.36	0.60,0.43, 0.53	0.64
25/15	520			0.58,0.58	
25	600		0.48,0.38	0.64,0.47, 0.59	0.62,0.38
30/20	640				0.62
30	720			0.43	0.44,0.43
35	840			0.35	0.35
40	960				0.29

7.4 DISCUSSION

In the first series of experiments, where root and shoot temperatures were the same, temperature was found to have a marked influence on the root regeneration potential (RRP) of *P. radiata* seedlings. The warm day/night temperature regimes ($21^{o}/16^{o}C$, $24^{o}/19^{o}C$, $27^{o}/22^{o}C$) were most beneficial for the proliferation of new roots. Maximum numbers (LR, SR, GT) and lengths (TL) of new root were produced at these temperatures (Fig. 7.1), with reduced root activity at the highest temperature ($30^{o}/25^{o}C$) and poorest root growth overall at the coolest temperature ($15^{o}/10^{o}C$). This root growth response to temperature agrees with an earlier but less comprehensive study on *P. radiata* seedlings by Macpherson (1970). In terms of numbers of active roots and root dry matter production, this author found that the RRP of root-pruned seedlings was equally good at temperatures of $18^{o}/13^{o}C$, $24^{o}/19^{o}C$ and $27^{o}/22^{o}C$, but, markedly reduced at $33^{o}/28^{o}C$. Macpherson's results, and the present results suggest that RRP of root-pruned and intact seedlings follows a similar response pattern at the same temperatures. Temperatures of $24^{o}/19^{o}C$ and $27^{o}/22^{o}C$ which promote the greatest root activity of intact seedlings (Macpherson, 1970) coincide with the temperatures at which the greatest RRP was observed in these experiments. Temperatures that encourage maximum RRP lie within the optimum temperature range for *P. radiata* seedling growth (Shepherd, 1965; Cremer, 1968; Florence and Malajczuk, 1970).

The reduced RRP of seedlings under the temperature regimes of $15^{o}/10^{o}C$ and $30^{o}/25^{o}C$ in Experiment 1 agrees not only with the poor root growth of intact seedlings at similar temperatures (Macpherson, 1970), but also with the overall reduction of growth of seedlings at temperatures of $15^{o}/10^{o}C$ or lower and of $30^{o}/25^{o}C$ or higher found by other authors (Shepherd, 1965; Cremer, 1968; Florence and Malajczuk, 1970). While the RRP of seedlings at $30^{o}/25^{o}C$ was less than at slightly lower temperatures it was not as low as for seedlings at $15^{o}/10^{o}C$. Root regeneration was markedly inhibited by cooler day/night temperatures.

Detailed information on the root growth activity of root-pruned or newly transplanted seedlings under various ambient temperatures is very limited in the literature. However, studies of intact

Pinus seedlings in the field and in controlled environments have shown that the numbers of actively growing root tips produced and the rates of root elongation are sensitive to high or low air temperatures (Turner, 1936; Bilan, 1967; Kozlowski, 1967; Merritt, 1968).

The day/night temperatures of $21^{o}/16^{o}C$, $24^{o}/19^{o}C$, $27^{o}/22^{o}C$ and $30^{o}/25^{o}C$ were more effective in promoting subsequent shoot growth of seedlings than a temperature of $15^{o}/10^{o}C$. The suppressed height growth of seedlings at $15^{o}/10^{o}C$, indicates a similar growth response to intact seedlings under the same temperature conditions, as described in the literature (Shepherd, 1965; Cremer, 1968; Florence and Malajczuk, 1970). The rate of height growth of seedlings at $15^{o}/10^{o}C$ was only statistically different from that of seedlings at $24^{o}/19^{o}C$ which grew the fastest. The slight increase in diameter growth of seedlings as well as root production at $15^{o}/10^{o}C$ suggests some photosynthates were available for growth. Root growth appeared to be favoured over shoot (height) growth.

In general, seedlings under the warmest temperatures $21^{o}/16^{o}C$, $24^{o}/19^{o}C$, $27^{o}/22^{o}C$ and even $30^{o}/25^{o}C$ show satisfactory growth after replanting. Temperatures of $15^{o}/10^{o}C$, however, are less favourable for subsequent growth. But, the second experiment showed that the shoot and roots of seedlings continue to grow at temperatures below $15^{o}/10^{o}C$, albeit at substantially reduced rates. Seedlings at temperatures of $11^{o}/6^{o}C$ and $8^{o}/4^{o}C$ had the potential to regenerate roots, but the subsequent extension of these new roots was inhibited. Shoot growth of intact seedlings was restricted at the lower temperatures, but, the presence of new roots suggests some photosynthates were channelled into the roots for growth. The better overall growth of seedlings at the higher temperatures could be a reflection of the greater amounts of photosynthates available for growth.

The pale unhealthy colour of the shoots of intact and root-pruned seedlings at the lowest temperature ($8^{o}/4^{o}C$) could be the result of nutrient deficiency. The restriction of mineral uptake and translocation of minerals in plants grown at low soil temperatures has been discussed by many authors, as cited by Knoll *et al.* (1964) and Cooper (1973). The exposure of plants to sixteen hours of cold night temperature in this treatment may have had a similar effect in disrupting their nutrition.

The general poor response of both intact and root-pruned seedlings to low temperature in this experiment fits closely to the

responses observed by Cremer (1968) who found the overall growth of seedlings was not favoured at temperatures of $9^{o}/4^{o}C$ and $12^{o}/7^{o}C$. Observations of other *Pinus* species in the field have shown that seasonal decreases in temperature limit both root and shoot growth of intact (Lanner, 1964; Bilan, 1967; Larson, 1967) and transplanted (Bilan, 1961) seedlings.

Decreasing night temperature under a favourable day temperature of $27^{o}C$ had little effect on the RRP of *P. radiata* seedlings. In terms of total numbers of root produced (GT, LR), the potential for root growth was the same under all the temperatures. However, differences were found in the subsequent extension of the new roots produced.

A greater proliferation of short roots (SR), a shorter length of LR (TL, AL), and a greater number of SR than LR were observed under the $10^{o}C$ night temperature (Fig. 7.6, Table 7.6). This response would indicate that a cool night temperature stimulates the proliferation of new roots but inhibits their subsequent extension. Production of equal numbers of SR and LR by seedlings under the $15^{o}/10^{o}C$ temperature regime in Experiment 1 would further suggest that cooler temperatures promote proliferation and to a lesser extent elongation of new roots.

There were no apparent trends in the length (TL) of root produced but the average length LR (AL) indicates that warmer nights of $22^{o}C$ were more beneficial in the extension of new roots than cooler nights of $10^{o}C$.

Previous work with *P. radiata* by Hellmers and Rook (1973) indicated that root growth was encouraged by cooler night temperatures. However, caution must be taken in comparing the growth responses of seedlings studied by these authors and the results of the present experiment. Because of the large differences in the actual treatment, there is really no basis for comparison. Seedlings used by Hellmers and Rook (1973) were growing intact under the various temperature regimes for three to six months before being harvested, whereas, seedlings in this experiment were root-pruned, and subjected to the various temperature regimes for a total of only five weeks. It is not surprising that the root response of seedlings in this study would not be as marked as the responses by seedlings in the study by Hellmers and Rook. Given time, perhaps comparable differences would result.

Diameter growth of seedlings was not influenced by night temperature, but, height growth was greater at the coolest night temperature. Relative rates of height growth showed that seedlings growing at 27^{o} day temperature and a 10^{o} night temperature were growing at a faster rate than seedlings at the 16^{o} night, but not significantly faster than seedlings at the 22^{o} night temperature. The responses obtained suggest that cooler night temperatures appear to favour shoot extension rather than root elongation, but, that warmer nights favour the overall better growth of seedlings. In other words, the distribution of growth within the seedlings was altered by the day and night temperature regime. It is tempting to speculate that the height response of seedlings under the $27^{o}/10^{o}C$ regime was due to seedling ability to conserve carbohydrates during the cool night. The duration of the $10^{o}C$ night temperature was for sixteen hours, ten of which were in the dark, possibly reducing the rates of respiration in the seedlings. The importance of low night temperatures for conserving food by reducing its use in respiration has been stressed by Kramer (1957).

Many reports have shown that cool soils stimulate the production of short, thick, white, succulent roots with few laterals and that warm soils stimulate the production of long, thin, brown roots with greater lateral production (Nightingale, 1935; Barney, 1951; Hellmers, 1963b; 1966; Larson, 1967; Lavender *et al.*, 1968; Bowen, 1970; Cooper, 1973; Rook and Hobbs, 1975; Abod, 1977). Observations on new root growth under the various temperature regimes presented here agree with these findings. The great differences in the number, length and morphological characteristics of the new roots produced suggests that soil temperature played a major part in the growth and development of the roots in all experiments. But, under the conditions of these earlier experiments the relative contribution of the air and soil to root growth could not be discerned.

In the second series of experiments the soil temperature was controlled separately. Air and soil temperatures were found to have separate and distinct effects on the root and shoot growth of both intact and root-pruned *P. radiata* seedlings. From the review by Cooper (1973) it is clear that root growth responses of plants to a range of temperatures can be characterized by sigmoid curves, with maximum growth occurring within an optimum temperature range which

varies with species. Based on the data from Experiments 1 to 13, it is evident that there is first of all a response surface to ambient temperature and, further, there is a response of *P. radiata* seedlings to each separate soil temperature. These resemble those observed for many other plant species (Cooper, 1973). That is, there was an optimum root temperature range for growth within each ambient air temperature regime.

For a given air temperature, maximum root growth occurred at soil temperatures which had more or less the same heat sum for that particular air temperature. This optimum root temperature varied with the air temperature. For example, in terms of numbers and lengths of new roots produced, maximum growth under the $15^{o}/10^{o}C$ air temperature was at a soil heat sum of 280 to 360 degree-hours, but, under the $25^{o}/15^{o}C$ air temperature at 480 to 600 degree-hours. The best RRP and root growth of intact seedlings occurred within the soil temperature range of $20^{o}C$ to $30^{o}C$.

The shoot (diameter and height) growth patterns were similar to those of the roots, although, the optimum range for shoot growth was generally wider than for root growth, for both intact and root-pruned seedlings. In this regard, soil temperature appeared to be less critical for shoot than for root growth, particularly within the higher temperature range.

A number of studies reported in the literature have also shown that the optimum soil temperatures for shoot and root growth of intact seedlings of the same species, and for both intact and root-severed seedlings of some species, lie within the same range (Adams, 1934; Barney, 1951; Stone and Schubert, 1958, 1959a,b; Hellmers, 1963b; Stone *et al.*, 1962; Steinbrenner and Rediske, 1964; Schubert and Baron, 1965; Chalupa and Fraser, 1968; Bowen, 1970; Larson, 1970; Lavender and Overton, 1972; Heninger, 1974; Heninger and White, 1974; Abod, 1977).

The marked differences in the numbers, lengths, sizes and colour of roots produced at the various soil temperatures conform with other reports in the literature (Nightingale, 1935; Barney, 1951; Schubert and Baron, 1965; Chalupa and Fraser, 1968; Bowen, 1970; Cooper, 1973; Rook and Hobbs, 1975; Abod, 1977). Detailed observation showed that within the optimum temperature range, large numbers of long, thin, brown roots were produced and that the cool soils outside the optimum range resulted in production of only a few, short, thick, white roots.

Growth inhibition at the low and high air and soil temperatures and the marked morphogenic differences in the new roots produced may have been a direct effect of temperature on root metabolism and synthesis of various growth factors (Street, 1966; Lavender and Overton, 1972; Atkin *et al.*, 1973; Lavender *et al.*, 1973).

The highest air and soil temperatures studied were most detrimental to root growth of both intact and root-pruned seedlings. At the 40°C soil temperature root systems of the intact seedlings appeared inactive and the root-pruned seedlings lacked the potential to regenerate new roots. Barney (1951) noted that at a soil temperature of 35°C roots of intact *Pinus taeda* seedlings also had an appearance of dormancy, and suggested that actual changes to the protoplasmic structure of the root might occur at supraoptimal temperatures. The increased shoot growth of intact seedlings at this high soil temperature indicates that all growth was not inhibited, but rather the distribution of growth was altered in favour of shoot rather than root growth. Because roots depend on shoots for carbohydrates and shoots depend on roots for water and minerals, the growth of both is closely coordinated (Nielson and Humphries, 1966). As roots are a carbohydrate sink and their growth is regulated by shoot activity it would appear that at the higher temperatures more food was available for the shoot than the root. It is generally recognized that the carbohydrates produced by the shoot are used preferentially for shoot growth with roots receiving the excess not used in the upper stem (Kozlowski and Keller, 1966). The sharp decline in roots produced at the higher temperature suggests perhaps the translocation of photosynthates was reduced to the roots and that more was available for shoot growth. High temperatures may however also have an effect by increasing respiration, hastening depletion of food reserves and consequently reducing the availability of photosynthates for the roots (Kramer, 1957; Kramer and Kozlowski, 1960). Alternatively, the high temperature may have affected the rate of photosynthesis (Wood and Brittain, 1973).

At the low air temperatures, root growth was preferred to height growth in both intact and root-pruned seedlings. The large numbers and lengths of thick , new roots produced and the larger stem diameter of root-pruned seedlings at the cool soils (10°, 15°C) could be a reflection of the greater amount of photosynthate present for

growth. Increasing air temperatures, enhanced the shoot growth and reduced the root growth of seedlings at the cool soil temperatures, reversing the pattern of growth distribution.

The high RRP of root-pruned seedlings and equally good shoot growth within the optimum temperature range suggests that the rates of photosynthesis, rates of translocation of photosynthates to the roots and the rate of utilization of photosynthates within the plant is at a maximum. The observed variation beyond the optimum range could be the result of changes in one of these, or a combination of these processes. Changes in these processes (photosynthesis, translocation) to variations in temperature have been reported for many other species in the literature (Decker, 1944; Crafts, 1951; Richardson, 1953b, 1956; Vinokur, 1957; Kozlowski and Keller, 1966; Negisi, 1966; Babalola *et al.*, 1968; Wood and Brittain, 1973; Turner and Jarvis, 1975).

Reduced overall growth at the temperature extremes might have involved a number of complicated interactions of water relations and nutrition besides the availability of photosynthates for growth. Low soil temperatures, in the order of 5^{o}-10^{o}C, have been reported to restrict the absorption of water (Duncan and Cooke, 1932; Kramer, 1940, 1942, 1956; Kozlowski, 1943; Böhning and Lusanandana, 1952; Rahman *et al.*, 1959; Ashby, 1960; Kuiper, 1964; Kramer, 1969; Cooper, 1973) and mineral uptake (Vinokur, 1957; Ashby, 1960; Power *et al.*, 1963; Bowen, 1970) in plants. This suggests that perhaps seedlings at low soil temperatures could have been under some nutrient or moisture stress. None of the seedlings in this study, however, showed signs of nutrient deficiency. In addition, previous experiments (Chapter 4) have indicated that the nutrients present in plants before root-pruning is sufficient to support growth for the period of study (three weeks), discounting the possibility that lack of nutrients was responsible for reduced growth.

Various degrees of needle desiccation on root-pruned seedlings at the soil temperatures examined suggested that these seedlings suffered some moisture stress. Intact seedlings suffered no needle desiccation which was perhaps just a reflection of the greater absorbing area of these seedlings. At increased air and soil temperatures it might be expected that moisture stress would be increased by seedlings due to rates of transpiration (e.g. Babalola *et al.*, 1968;

Cooper, 1973; Rook and Hobbs, 1975). Death of two root-pruned seedlings at the highest temperatures in contrast to the continued growth of intact seedlings suggests that severe moisture stress might have developed in these seedlings due to the absence of roots. This question is explored further in subsequent chapters.

The results of this long series of experiments show that both air and soil temperatures are important factors controlling the RRP and subsequent shoot growth of root-pruned *P. radiata* seedlings. Although root responses are shown to be more related to the soil than to the air temperature, there is a clear trend for air temperature to alter the distribution in growth in such a way that root growth is favoured at the lower temperature range. Shoot growth on the other hand, is more related to air temperature and less critical of temperatures of the root zone.

In particular, the best growth response of *P. radiata* occurs in the warm air and soil temperature range (20^{o}-30^{o}C) with a heat sum equivalent of 480 to 720 degree-hours. This applies to temperature experiments with both controlled (Experiments 4 to 13) and uncontrolled (Experiments 1 to 3) soil temperatures, despite the fact that there were differences in the ages, sizes and growth history of the seedlings and the environmental conditions themselves. Since under both controlled and uncontrolled soil temperature experiments various combinations of actual temperature and temperature duration were used, the consistent occurrence of maximum growth within the same soil heat sum range suggests that daily soil heat sum is a critical factor influencing root growth.

Nevertheless, the relative proportion of various root types (short roots (SR) and long roots (LR)) produced varied with the actual temperature regime. Under cooler air and soil temperatures more SR were produced than LR. This has also been shown in a previous experiment (Chapter 4).

The varied growth patterns found over the temperature range can be of practical importance in silvicultural work in relation to nursery practice and plantation establishment. In the nursery, wrenching, root-pruning and fertilization, for example, should be undertaken at the time of the year when temperature conditions are favourable for RRP. In this regard such practices such as undercutting and/or wrenching should be avoided particularly where soil temperatures are too low, or for that matter too high, since seedling growth and even survival could be impaired.

Cool air temperatures and warm soils, characteristic of autumn, winter and early spring would favour root production. Although a large portion of the roots would be shorter, they should retain their potential to elongate (Stone and Schubert, 1959a). In addition, under these conditions, stockier (smaller height:diameter ratio) and better balanced (greater root:shoot ratio) seedlings could be attained, features which are welcomed in seedling production.

CHAPTER 8

THE EFFECT OF AIR AND SOIL TEMPERATURE ON PHOTOSYNTHESIS, TRANSLOCATION OF PHOTOSYNTHATES AND WATER RELATIONS OF SEEDLINGS

8.1 INTRODUCTION

In the previous chapter it was shown that marked differences in seedling growth occurred at various air and soil temperatures. It was also suggested that the root growth response might have been related to differences in the rates of photosynthesis, in the translocation of photosynthates or in the water relations of the seedlings. These possibilities are explored in this chapter. The work described was carried out in conjunction with the soil temperature experiments described in Chapter 7 (Section 7.3).

8.2 EFFECT OF VARIOUS AIR AND SOIL TEMPERATURES ON PHOTOSYNTHESIS OF INTACT AND ROOT-PRUNED SEEDLINGS

8.2.1 Materials and Methods

Photosynthesis measurements were carried out on seedlings just prior to the final harvest, that is, three weeks after root-pruning had taken place. Two intact and two root-pruned seedlings from each temperature treatment (see Table 7.7) were selected for photosynthesis measurement. In addition, two intact and root-pruned seedlings at the ambient soil temperatures of $15^{o}/5^{o}C$ (Experiment 5) and $20^{o}/10^{o}C$ (Experiment 8) were included in the measurement.

Photosynthesis was measured by infra-red gas analysis, as detailed in Chapter 3 (Section 3.2.3). Measurement took place at the day air temperature at which the seedlings were growing while roots were maintained at the treatment soil temperature. Light intensity was adjusted to approximately $735\mu Em^{-2}sec^{-1}$ (3500 f.c.) for measurement.

Net photosynthesis was calculated as mg CO_2/g/hr (see Chapter 3, Section 3.5.1). where the weight is dry weight of green needles. All desiccated portions of needles were excluded.

8.2.2 Statistical Analysis

Differences in the rates of photosynthesis were compared between the treatments of the same experiment. Comparisons were not made between experiments or between intact and root-pruned seedlings. Duncan's multiple range test was used to test the differences between treatment means in Experiments 4, 5, 6, 8, 9, 10, 11, 12, 13. Student's t-test was used to compare the differences between the treatment means in Experiment 7. The results of the analyses are presented in Appendix V. The statistical analyses must obviously have limited usefulness because of the very small number of plants involved, only two per treatment, but have been included for completeness.

8.2.3 Results

The results of the effect of various air and soil temperatures on the rates of photosynthesis of root-pruned and intact seedlings are summarized in Tables 8.1 and 8.2 respectively. Intact seedlings had consistently higher rates of net photosynthesis, however, the patterns of photosynthetic response under the various temperature regimes were similar for both intact and root-pruned seedlings (Figure 8.1).

Photosynthetic rates of both intact and root-pruned seedlings were very similar for most soil temperatures tested for a given air temperature regime. However, there were some interesting trends observed in relation to increasing soil and air temperature.

Under the $15^{o}/5^{o}C$ and $20^{o}/10^{o}C$ air temperature regimes, net photosynthesis tended to increase with increases in soil temperature. At these temperatures RRP is also high. Under the $25^{o}/15^{o}C$ air temperature, photosynthesis rates were significantly reduced where the soil temperature was only $10^{o}C$ but apart from a slight decline at soil temperatures of $30^{o}C$ and $35^{o}C$, the rates at other soil temperatures varied little. Under the highest air temperature ($30^{o}/20^{o}C$) there was a tendency for photosynthesis of root-pruned seedlings to increase with decreasing soil temperature in Experiment 12, but, a contrary result is shown Experiment 13 so that there was no clear trend. The values at all soil temperatures up to $35^{o}C$ were high for both root-pruned and intact seedlings. As very little root growth occurred at root temperatures above $30^{o}C$, it seems that the photosynthates produced must have been used other than in root growth.

Table 8.1 Net photosynthesis of root-pruned seedlings after three weeks at various air and soil temperatures. The values in $mg.g^{-1}.hr^{-1}$ are the means of 2 replicates.

Soil Temperature (°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	3.16			
10	240	4.62	7.32	3.09	
15/5	280	6.83,5.32			
15	360	6.84	5.48	3.46	9.72
20/10	400		6.11,4.30		
20	480	6.85	9.54,5.90	3.46,6.89, 3.32	7.53
25/15	520			3.67,7.92	
25	600		11.08,5.83	3.86,6.51, 6.53	7.19,4.47
30/20	640				7.30
30	720			5.00	6.31,7.70
35	840			5.29	7.59
40	960				4.49

Table 8.2 Net photosynthesis of intact seedlings after three weeks at various air and soil temperatures. The values in $mg.g^{-1}.hr^{-1}$ are the means of 2 replicates.

Soil Temperature(°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	4.58			
10	240	7.77	9.22	7.16	
15/5	280	10.78,10.68			
15	360	12.82	7.11	9.72	8.71
20/10	400		9.45,5.92		
20	480	9.32	13.80,7.04	10.03,9.48, 9.11	7.13
25/15	520			10.27,11.32	
25	600		11.16,6.25	10.92,6.19, 9.24	9.70,7.74
30/20	640				9.56
30	720			5.89	9.04,9.25
35	840			7.29	7.44
40	960				5.82

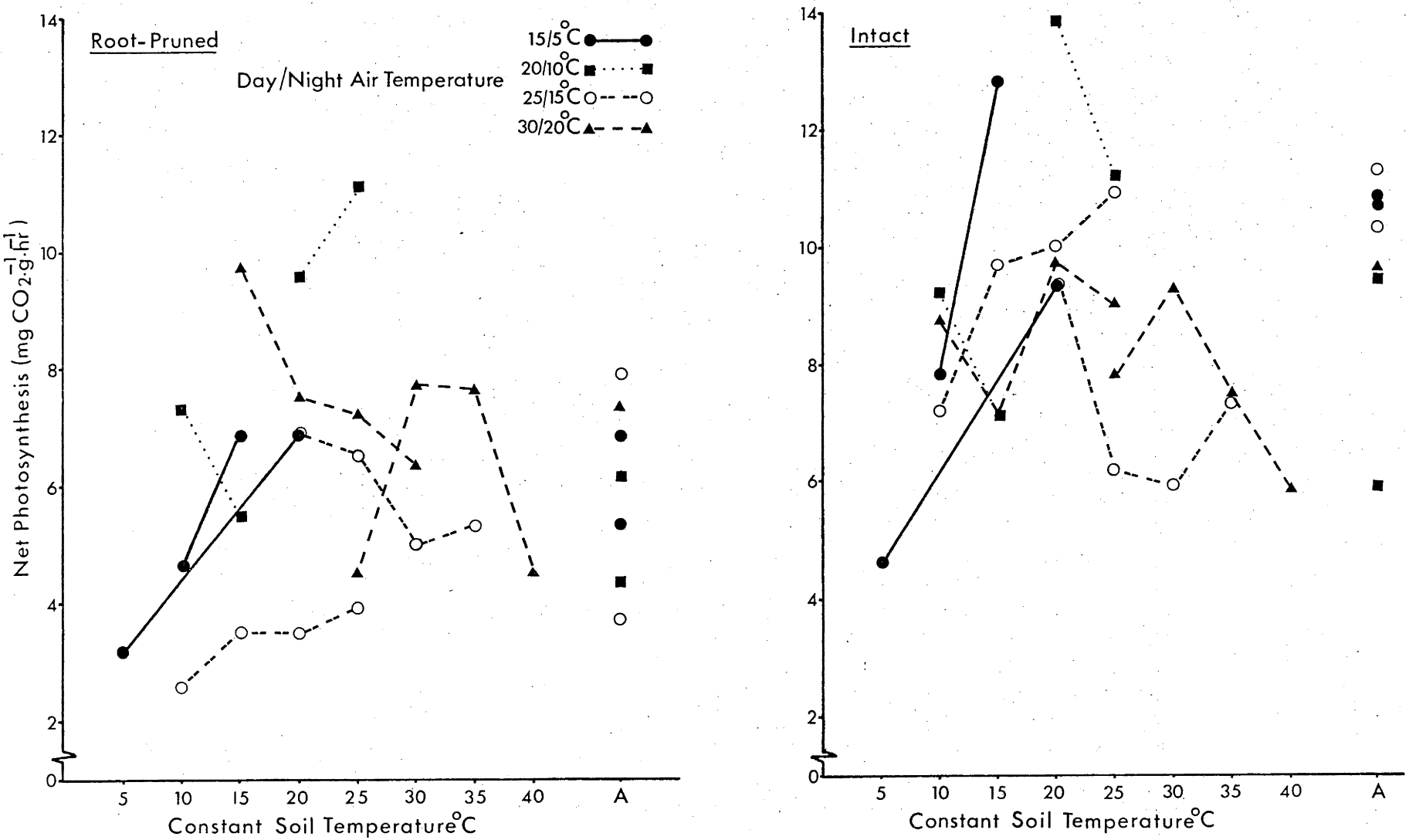

Figure 8.1. Effect of various air and soil temperatures on net photosynthesis of root-pruned and intact seedlings. Lines join constant soil temperature treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

At soil temperatures of 40°C rates of photosynthesis of both intact and root-pruned seedlings was significantly reduced as was root growth.

Air temperature had less apparent influence on photosynthesis than soil temperature. Even at the lowest air temperature of 15°/5°C, high rates of photosynthesis were attained with warm soils. For intact seedlings photosynthesis was relatively high under all air temperatures, but, was markedly reduced at a soil temperature of 5°C under the 15°/5°C air temperature with a tendency for a reduced rate at 10°C soil under the same air temperature regime.

8.3 EFFECT OF VARIOUS AIR AND SOIL TEMPERATURES ON THE TRANSLOCATION OF ^{14}C-LABELLED PHOTOSYNTHATES IN BOTH INTACT AND ROOT-PRUNED SEEDLINGS

8.3.1 Materials and Methods

Three root-pruned seedlings and the two intact seedlings were selected for assessing translocation of ^{14}C-photosynthate at each soil temperature regime in Experiments 4, 5, 6, 7, 9, 10 and 12 of Chapter 7. The apparatus used in ^{14}C-labelling is detailed in Chapter 3 (Section 3.2.4).

The shoot of each seedling was exposed to $^{14}CO_2$ just prior to being placed into the various soil temperatures. Root-pruned seedlings were fed no later than 10-15 minutes after the roots were severed. At harvest, three weeks later, after appropriate root and shoot measurements were made, the plant parts were separated into main stem, branches, residual root (total final root minus new root) and new roots then oven-dried (see Chapter 3, Section 3.3.5). Samples were prepared and radioactivity counted as detailed in Chapter 3 (Section 3.2.4). The proportion of ^{14}C-photosynthate accumulated in each plant part was calculated as described in Chapter 3 (Section 3.5).

8.3.2 Statistical Analysis

Duncan's multiple range test (Experiment 4, 6, 9, 10, 12) and Student's t-test (Experiments 5, 7) were used in comparing differences between treatment means. Differences in the means between experiments and between intact and root-pruned seedlings were not compared. The results of the analyses are presented in Appendix VI. Once again the limited number of observations possibly limits the usefulness of such analyses.

8.3.3 Results

The proportion of ^{14}C accumulated in the total shoot (main stem and branches) and total root (new and residual root) of root-pruned and intact seedlings are summarized in Tables 8.3, 8.4 and Tables 8.5, 8.6 respectively. The results of the distribution of assimilates into the main stem, branches, residual root and new root are presented in Appendix VI. Substantial plant to plant variation was evident in both root-pruned and intact seedlings but the pattern of ^{14}C distribution did show quite consistent trends in relation to air and soil temperature.

The most striking difference in ^{14}C distribution was between root-pruned and intact seedlings (Figures 8.2 and 8.3). In all treatments root-pruning resulted in reduced ^{14}C-photosynthate accumulation by the roots, the results for root-pruned and intact seedlings will be presented separately.

a) Root-pruned Seedlings

The greatest proportion of photosynthate accumulated by the roots was under the lowest air temperature (Table 8.4, Figure 8.2). This pattern of ^{14}C-photosynthate distribution indicated more photosynthate was translocated away from the shoots where height growth was suppressed. Increasing air temperature resulted in marked reductions in photosynthate in the roots (Tables 8.4 and 8.5), which paralleled shoot growth increases at these temperatures. The relatively small accumulation of ^{14}C in the branches of seedlings (Appendix VI) under this air temperature indicates most photosynthates were held in the stem. Diameter growth was greater at these temperatures.

Under the $20^{o}/10^{o}C$ air temperature, translocation of photosynthates to the roots was markedly reduced by a soil temperature of $10^{o}C$. The same tendency was shown under the $15^{o}/5^{o}C$ and $25^{o}/15^{o}C$ air temperature regimes.

Under the $25^{o}/15^{o}C$ air temperature the proportion of photosynthates accumulated by the roots was high at the high soil temperatures of $30^{o}C$ and $35^{o}C$, but at a soil temperature of $35^{o}C$ root growth had virtually ceased and shoot growth was suppressed. The proportion of ^{14}C-photosynthates in new roots (Appendix VI) under this air temperature was higher at the $25^{o}C$ soil temperature than any other.

Table 8.3 Proportion of ^{14}C-photosynthate accumulated in the shoots of root-pruned seedlings three weeks after ^{14}C-labelling. The values expressed as percentage of total plant ^{14}C recovery are the means of 3 replicates.

Soil Temperature(^{o}C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (^{o}C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	86.7			
10	240	78.0	92.3	94.0	
15/5	280	78.8			
15	360	74.6	82.1	92.0	88.3
20/10	400		87.8		
20	480	78.7	83.1	87.4,89.4	87.9
25/15	520			89.9	
25	600		78.1	88.6,91.2	84.0
30/20	640				88.0
30	720			85.1	87.7
35	840			85.3	
40	960				

Table 8.4 Proportion of ^{14}C-photosynthate accumulated in the roots of root-pruned seedlings three weeks after ^{14}C-labelling. The values expressed as percentage of total plant ^{14}C recovery are the means of 3 replicates.

Soil Temperature(°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	10.1			
10	240	22.3	7.7	6.0	
15/5	280	20.7			
15	360	25.4	18.0	8.1	11.4
20/10	400		12.2		
20	480	21.3	16.9	12.5,10.5	12.1
25/15	520			10.1	
25	600		21.9	11.7,8.8	16.0
30/20	640				11.7
30	720			14.9	12.3
35	840			14.7	
40	960				

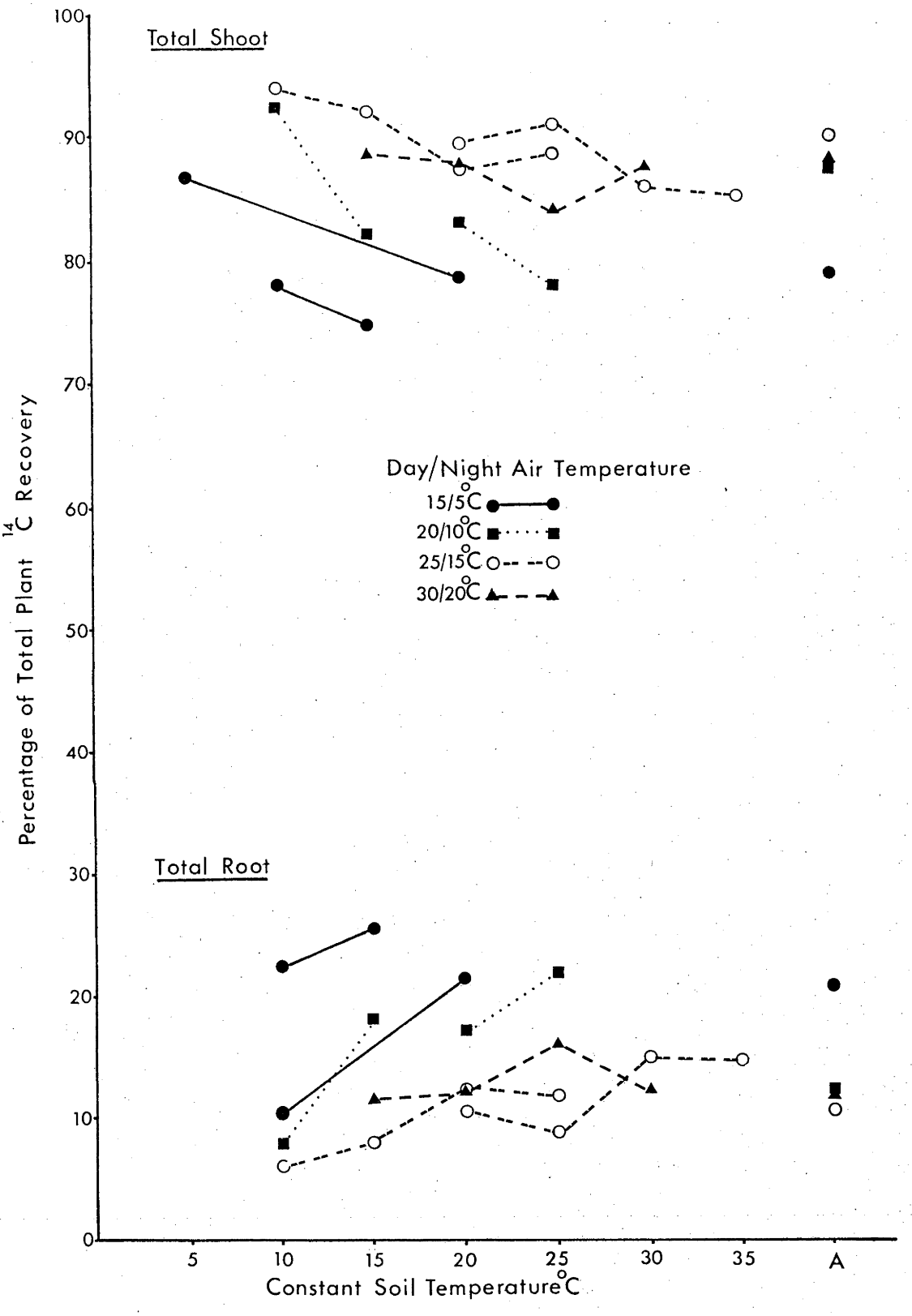

Figure 8.2. Translocation of ^{14}C-labelled photosynthate to the shoots and roots of root-pruned seedlings at different air and soil temperatures. Lines connect treatments of the same experiment. 'A' indicates soil temperatures the same as air temperature.

Table 8.5 Proportion of ^{14}C-photosynthate accumulated in the shoots of intact seedlings three weeks after ^{14}C-labelling. The values expressed as percentage of total plant ^{14}C recovery are the means of 2 replicates.

Soil Temperature(^{o}C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (^{o}C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	67.2			
10	240	70.2	80.1	80.0	
15/5	280	66.1			
15	360	61.0	75.1	78.2	69.0
20/10	400		73.0		
20	480	58.2	65.8	73.8,84.0	72.5
25/15	520			75.5	
25	600		70.8	71.8,74.1	65.9
30/20	640				71.0
30	720			73.1	74.5
35	840			72.3	
40	960				

Table 8.6 Proportion of ^{14}C-photosynthate accumulated in the roots of intact seedlings three weeks after ^{14}C-labelling. The values expressed as percentage of total plant ^{14}C recovery are the means of 2 replicates.

Soil Temperature (^{o}C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (^{o}C)			
		$^{15}/_{5}$	$^{20}/_{10}$	$^{25}/_{15}$	$^{30}/_{20}$
5	120	32.6			
10	240	29.9	20.0	20.7	
15/5	280	34.0			
15	360	39.0	24.7	21.8	31.0
20/10	400		27.0		
20	480	41.6	34.2	26.1,16.0	27.5
25/15	520			24.4	
25	600		29.2	28.2,25.9	34.1
30/20	640				28.3
30	720			26.8	25.6
35	840			27.7	
40	960				

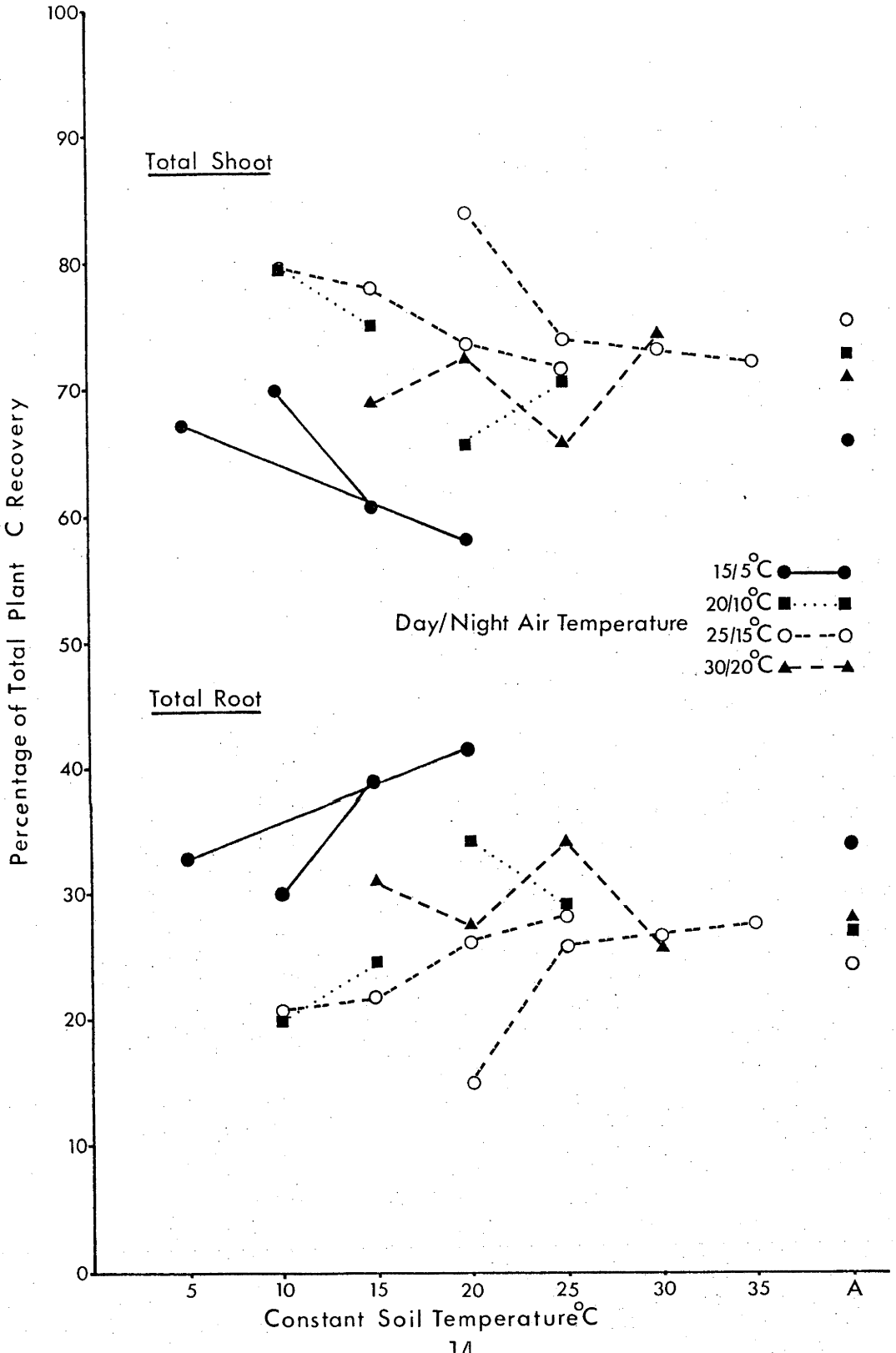

Figure 8.3. Translocation of ^{14}C-labelled photosynthate to the shoots and roots of intact seedlings at different air and soil temperatures. Lines connect treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

Under the highest air temperature ($30^{o}/20^{o}C$) soil temperatures of $15^{o}C$ to $30^{o}C$ made no great difference to the amount of ^{14}C-photosynthates translocated to the roots but a greater proportion of ^{14}C occurred in new roots at soil temperatures of $20^{o}C$ and $25^{o}C$.

b) Intact Seedlings

The proportion of ^{14}C-assimilates accumulated by roots of intact seedlings was also high at the low air temperature (Tables 8.5 and 8.6). At the high air temperature ($30^{o}/20^{o}C$) translocation to the roots was slightly reduced, though not significantly, by a soil temperature of $30^{o}C$.

Interestingly, in new roots (Appendix VI) there is a greater accumulation of ^{14}C-photosynthates at the lower than at the higher soil temperatures under the $15^{o}/5^{o}C$, $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures. For example, under the $25^{o}/15^{o}C$ air temperature, greater ^{14}C-accumulation occurred at the $10^{o}C$ soil temperature than any other.

8.4 EFFECT OF VARIOUS AIR AND SOIL TEMPERATURES ON NEEDLE DESICCATION AND RELATIVE NEEDLE WATER CONTENT OF SEEDLINGS

8.4.1 Materials and Methods

8.4.1.1 Needle Desiccation

The two root-pruned seedlings used for photosynthesis measurement at each soil temperature in Experiments 4 to 13 (Chapter 7) were also used for determination of stem and branch needle desiccation. Intact seedling needles did not desiccate. At harvest, all dried needles or needle tips were removed from the seedlings. Primary needles of the stem and branches were usually totally dried, but, only the portion closest to the needle tip was desiccated on secondary needles. The portions of green needle and dried needle of the stem and branch leaves were oven-dried separately and weighed. Per cent needle desiccation was determined for stem and branch leaves on a dry weight basis as follows:

$$ND = \frac{GN}{GN+DN} \times 100$$

where ND = needle desiccation in per cent.

GN = oven dry weight of green needle in grams.

DN = oven dry weight of dried needle in grams.

8.4.1.2 Relative Water Content of Needles (RNWC)

The relative water content of needles (Clausen and Kozlowski, 1965) was calculated for intact and root-pruned seedlings in each soil temperature treatment in Experiments 4 to 13 (Chapter 7) as follows:

$$RNWC = \frac{FN - DN}{SN - DN} \times 100$$

where RNWC = relative water content of needles in per cent.
FN = fresh weight of whole needle in grams.
DN = oven dry weight of whole needle in grams.
SN = saturated weight of whole needle in grams.

RNWC measurements were made, a) on intact seedlings prior to root-pruning and placing the seedlings into the various treatments, b) after one week at the various soil temperatures and c) at the harvest, after three weeks at the various soil temperatures. Three fascicular needles were selected from each of two randomly selected seedlings at each measurement time. Needles were selected at mid-height of the seedlings at least two hours after morning watering. Desiccated needle portions were not removed in determining RNWC of root-pruned seedlings. The values recorded for these seedlings, therefore, were not solely the result of temperature, rather, temperature plus needle desiccation.

Fresh weight was obtained by weighing needles immediately after removal. Needles were then placed on end in test-tubes containing small amounts of distilled water. The test-tubes were then securely plugged and needles allowed to saturate under low light at room temperature.

After 24 hours the needles were removed from the test-tubes, dried quickly with absorbent paper and weighed. After the saturated needles were dried for at least 24 hours, oven dry weights were measured and RNWC calculated.

8.4.2 Statistical Analysis

Differences in ND and RNWC between treatments were compared using Duncan's multiple range test or Student's t-test. No comparisons were made between the various experiments or between the intact or root-pruned seedlings. The results of the analyses for percentage stem and branch needle desiccation are presented in Appendix VIIA.

The measurements of RNWC were analysed two ways, (i) to determine the differences in RNWC between the soil temperature treatments at one and three weeks after treatment and (ii) to determine the change in RNWC with time for each soil temperature. The results of the analyses of (i) and (ii) are presented in Table 8.9 and Appendix VIIB respectively.

8.4.3 Results

8.4.3.1 Needle Desiccation

The percentage needle desiccation of the stem and branch needles are summarized in Table 8.7 and 8.8 respectively. Low air temperature ($15^{o}/5^{o}C$), regardless of soil temperature, resulted in the least proportion of dried needles (Figure 8.4). Increasing air temperature substantially increased desiccation, with the greatest proportion of dried needles found under the $25^{o}/15^{o}C$ air temperature regime.

Soil temperature had a major influence on the proportion of needles desiccated regardless of air temperature. Low soil temperatures of 10^{o} and $15^{o}C$ under the $25^{o}/15^{o}C$ air temperature and of 15^{o} and $20^{o}C$ under the $30^{o}/20^{o}C$ air temperature resulted in significant increases in needle desiccation. The proportion of dried needles at a soil temperature of $15^{o}C$ under the $30^{o}/20^{o}C$ air temperature was almost double that found at soil temperatures of $25^{o}C$. But, despite this loss of green needle weight (over 50%), net photosynthesis for these seedlings was high.

High air temperatures ($25^{o}/15^{o}C$, $30^{o}/20^{o}C$) combined with high soil temperatures also increased needle desiccation and soil temperatures above $30^{o}C$ increased desiccation markedly. The lowest proportion of desiccation tended to occur at soil temperatures where the soil heat sum was more or less equivalent to the air heat sum (see Tables 8.7 and 8.8).

8.4.3.2 Relative Water Content of Needles (RNWC)

Marked differences were found in RNWC of both intact and root-pruned seedlings after the first and third week under various air and soil temperatures (Table 8.9). Changes in RNWC also occurred at each soil temperature with time (Appendix VIIB). The results for root-pruned and intact seedlings are presented separately.

Table 8.7 Percentage stem needle desiccation of root-pruned seedlings three weeks after replanting under various air and soil temperatures. Values are means of 2 replicates.

Soil Temperature(°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	22.41			
10	240	27.81	65.00	70.28	
15/5	280	19.53			
15	360	27.50	35.79	63.25	57.26
20/10	400		51.93		
20	480	23.29	51.82	47.34,41.08	50.99
25/15	520			46.82	
25	600		45.10	50.24,41.44	29.44,36.68
30/20	640				26.83
30	720			38.55	41.24,34.91
35	840			51.75	47.18
40	960				59.62

Table 8.8 Percentage branch needle desiccation of root-pruned seedlings three weeks after replanting under various air and soil temperatures. Values are means of 2 replicates.

Soil Temperature(°C)	Daily Heat Sum of the Soil (degree-hours)	Ambient Day/Night Air Temperature (°C)			
		15/5	20/10	25/15	30/20
5	120	13.33			
10	240	32.50	60.10	59.88	
15/5	280	20.21			
15	360	22.38	15.02	49.80	56.07
20/10	400		48.12		
20	480	14.20	46.10	46.75,39.84	40.77
25/15	520			50.72	
25	600		35.92	46.70,21.12	27.22,39.90
30/20	640				30.32
30	720			24.32	37.42,36.16
35	840			44.60	40.0
40	960				61.70

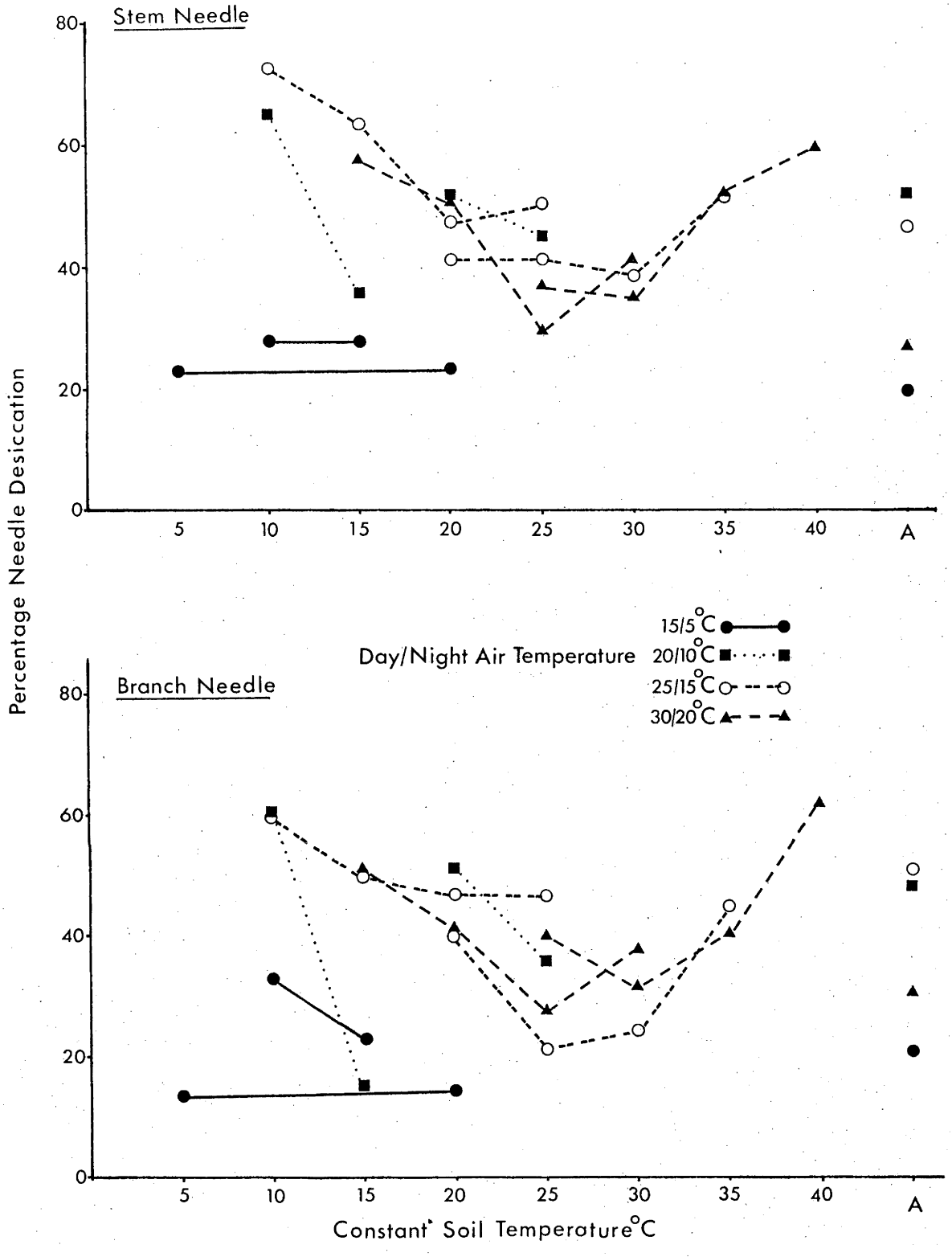

Figure 8.4. Percentage stem and branch needle desiccation of root-pruned seedlings, three weeks after replanting under various air and soil temperatures. Lines join treatments of the same experiment. 'A' indicates soil temperature the same as air temperature.

Table 8.9 Relative water content of needles of intact and root-pruned seedlings after one week and three weeks under various air and soil temperatures. Bracketed values indicate soil temperatures in °C. 'A' represents soil temperatures the same as air temperatures.

A. ROOT-PRUNED

Experiment Number	Day/Night Air Temperature(°C)	Relative Needle Water Content (%)[1]		
		Initial (Intact) Measurement	After one week	After three weeks
4	15/5	85.9	84.7 (A) 85.9 (10) 88.6 (15)	85.9 (15) 86.4 (A) 86.4 (10)
5	15/5	90.6	87.6 (20) 89.2 (5)	82.7 (20) 85.3 (5)
6	20/10	86.6	73.2 (10) 75.8 (15) 85.5 (A)	71.3 (10) 77.9 (15) 78.6 (A)
7	20/10	86.9	87.0 (20) 88.7 (25)	87.7 (20) 89.6 (25)
8	20/10	89.3	76.9 (20) 82.8 (25)	71.6 (25) 74.8 (20)
9	25/15	89.9	74.3 (15) 76.3 (20) 76.8 (10) 80.0 (25) 82.70 (A)	64.6 (15) 70.8 (10) 78.8 (A) 80.0 (25) 80.5 (20)
10	25/15	88.0	74.4 (20) 79.6 (30) 79.7 (35) 81.2 (25)	78.1 (25) 79.8 (30) 80.5 (35) 83.2 (20)
11	25/15	85.9	69.2 (25) 74.9 (A) 75.9 (20)	74.9 (A) 76.8 (20) 77.9 (25)
12	30/20	88.7	69.7 (15) 69.9 (20) 73.4 (30) 75.7 (25) 76.6 (A)	65.7 (15) 71.2 (20) 75.2 (25) 75.5 (30) 81.4 (A)
13	30/20	86.9	79.2 (25) 80.2 (30) 82.6 (40) 82.9 (35)	73.0 (40) 74.0 (30) 74.5 (25) 79.0 (35)

B. INTACT

4	15/5	85.9	85.7 (10) 87.7 (A) 90.5 (15)	86.6 (10) 90.7 (A) 91.4 (15)
5	15/5	90.6	87.8 (5) 91.7 (20)	85.5 (5) 90.0 (20)
6	20/10	86.6	84.1 (10) 86.6 (15) 90.6 (A)	87.2 (10) 87.6 (A) 91.1 (15)
7	20/10	86.9	85.1 (25) 85.2 (20)	85.1 (25) 86.7 (20)
8	20/10	89.3	84.0 (25) 86.3 (20)	85.9 (20) 86.0 (25)
9	25/15	89.9	85.3 (10) 86.8 (15) 87.1 (A) 87.7 (20) 88.0 (25)	83.2 (10) 84.0 (25) 84.2 (20) 84.2 (A) 84.9 (15)
10	25/15	88.0	86.0 (20) 86.6 (30) 86.6 (35) 88.6 (25)	86.7 (30) 87.1 (35) 89.3 (20) 89.7 (25)
11	25/15	85.9	85.0 (25) 86.0 (20) 87.3 (A)	86.6 (A) 87.3 (20) 87.6 (25)
12	30/20	88.7	83.2 (15) 84.1 (20) 85.6 (30) 85.8 (A) 86.5 (25)	83.2 (15) 84.0 (20) 84.9 (A) 85.4 (25) 86.4 (30)
13	30/20	86.9	85.5 (25) 87.4 (35) 87.8 (30) 88.7 (40)	80.2 (25) 84.4 (35) 88.4 (30) 89.5 (40)

1 Mean value of 6 replicates.

Note: Horizontal lines join treatment means that are not significantly different at the $P_{0.05}$ significance level according to Duncan's multiple range test or Student's t-test.

a) Root-Pruned Seedlings

In Appendix VIIB results show that significant decreases in RNWC occurred in seedlings after pruning at ambient air temperatures of $20^{o}/10^{o}C$ and above. Reductions in RNWC were relatively minor at the low air temperature ($15^{o}/5^{o}C$). After one week at all of the higher air temperatures, low soil temperature ($10^{o}C$, $15^{o}C$) resulted in low RNWC values and the warmer soils (above $15^{o}C$) resulted in higher values (Table 8.9). At the highest air temperature ($30^{o}/20^{o}C$) root-pruned seedlings at the higher soil temperatures of $35^{o}C$ and $40^{o}C$ had high RNWC values, only a few percentage points less than the original values before root-pruning.

After three weeks the differences in RNWC between treatments were still evident and little changed. Some estimates changed markedly, but these were not consistent and could only be attributable to sampling errors. Only at the $30^{o}/20^{o}C$ air temperature and at the higher soil temperatures between $25^{o}C$ and $40^{o}C$ was there a clear trend towards somewhat lower RNWC values, values more in line with all of the other air regime values. The trend towards lower RNWC at low soil temperatures was, if anything, more marked.

b) Intact Seedlings

After one week there were differences in the RNWC of seedlings between treatments. That is, there was a tendency for lower RNWC at the lower soil temperatures, a trend which was still evident at the end of three weeks.

8.5 SUMMARY OF RESULTS

8.5.1 Net Photosynthesis

(i) The rates of photosynthesis of intact seedlings were higher than for root-pruned seedlings.

(ii) At low to medium air temperatures ($15^{o}/5^{o}C$, $20^{o}/10^{o}C$, $25^{o}/15^{o}C$) there was a trend of increasing photosynthesis with increasing soil temperature for both intact and root-pruned seedlings, with the highest values in soils with a heat sum more or less equivalent to the air heat sum.

(iii) Under the $25^{o}/15^{o}C$ and $30^{o}/20^{o}C$ air temperatures, photosynthetic rates of intact and root-pruned seedlings continued at high rates at soil temperatures of $30^{o}C$ and $35^{o}C$.

(iv) A soil temperature of $40^{o}C$ reduced photosynthesis of all seedlings, but more drastically in root-pruned than in intact seedlings.

8.5.2 Translocation of Photosynthates

(i) Root-pruning seedlings reduced the accumulation of photosynthates in the roots markedly in comparison to intact seedlings.

(ii) More ^{14}C was translocated to the roots at low air temperature regardless of soil temperature.

(iii) Low soil temperature under the $15^{o}/5^{o}C$, $20^{o}/10^{o}C$ and $25^{o}/15^{o}C$ air temperature reduced the proportion of photosynthates accumulated in the roots.

(iv) At a high soil temperature of $35^{o}C$ under a $25^{o}/15^{o}C$ air temperature significant translocation of ^{14}C-assimilates to the roots occurred even though very few roots developed.

8.5.3 Needle Desiccation and Relative Water Content of Needles

(i) Needle desiccation (stem and branch needles) of root-pruned seedlings was lowest under the low air temperature regime ($15^{o}/5^{o}C$).

(ii) Low soil temperature combined with high air temperature increased needle desiccation.

(iii) High soil temperature combined with high air temperature increased needle desiccation.

(iv) Generally, medium soil temperatures where the heat sums were more or less equivalent to the air heat sum showed the least desiccation.

(v) Root-pruning resulted in reductions in relative water content of the needles (RNWC) but more so under high air temperatures.

(vi) RNWC of both intact and root-pruned seedlings were lower at low soil temperatures and high at the medium to high soil temperatures under all air temperatures.

8.6 DISCUSSION

The results indicate that variations in both air and soil temperature had important effects on the rate of photosynthesis, on the translocation of photosynthates and on the water relations of the seedlings.

Within the lower range of the air temperatures tested ($15^{o}/5^{o}C$ - $25^{o}/15^{o}C$) the rate of photosynthesis increased with increasing soil temperature. This was true for both intact and root-pruned seedlings. However, at the higher air temperatures there was little influence of soil temperature, apart from the depressing effect of the highest soil temperature of $40^{o}C$. Thus photosynthesis may be near optimal at almost any point within the medium soil temperature range ($15^{o}C$ to $30^{o}C$). Studies by a number of authors have shown that high rates of photosynthesis for many conifers occur within this soil temperature range (Babalola *et al.*, 1968; Vogl *et al.*, 1972; Rook and Hobbs, 1975; Abod, 1977). The most favourable air temperatures for photosynthesis were also found to lie within this same range, consistent with previous findings for the species by Wood and Brittain (1973).

A strong correlation between current photosynthate production by the shoot and root elongation has been shown by Wassink and Richardson (1951), Richardson (1953a,b, 1956), Eliasson (1968) and Webb (1976). These researchers have found that any change in the environment of the shoot which causes a change in the rate of photosynthesis, including temperature and light intensity, has a commensurate effect on the rate of root elongation and growth. These reported findings together with rates of photosynthesis observed in this study suggest that the greater elongation and growth of roots noted in Chapter 7 is related to near optimal photosynthesis at these temperatures.

The observed differences in the rates of photosynthesis between intact and root-pruned seedlings was not surprising. The severing of the roots must result in a gross physiological change in the seedlings. Humphries and Thorne (1964) and Abod (1977) have reported that root severence reduces photosynthesis in plants. The present observations were made only at one point in time, three weeks after the roots were pruned. Given that full recovery of photosynthetic activity would gradually occur it would be interesting now to observe the time course of this recovery. Three weeks after pruning many new roots had developed but photosynthesis was still low. It could be very low indeed immediately after root-pruning. These questions relating to recovery of photosynthesis are explored further in the next chapter.

Of the air temperatures examined, more photosynthate accumulated in the roots under the lowest air temperature ($15^{o}/5^{o}C$)

where shoot growth was limited. These results are in agreement with other work which has shown that the root system is a major sink for photosynthates produced when shoot activity has declined (Mochizuki and Hanada, 1957; Nelson,1964; Priestley, 1964; Hansen, 1967; Gordon and Larson, 1968; Quinlan, 1969; Schier, 1970; Jenkins, 1975; Rook and Hobbs, 1975). The increased stem diameter at this low air temperature suggests, however, that all food was not channelled to the roots as a significant amount is apparently diverted into stem cambial growth. The proportion of ^{14}C accumulated in the branches was low, also suggesting preferential distribution to the stem.

The greatest accumulation of ^{14}C-photosynthate in the roots occurred at soil temperatures ranging between 15°C and 30°C under the air temperatures examined. High photosynthesis rates and translocation of assimilates to the roots are in agreement with the observed increase in root growth at these temperatures. Research on translocation in relation to air and soil temperature is generally not precise (Nelson, 1963; Wardlaw, 1968). However, there is evidence from work by Burr *et al.* (1958) with sugar cane, Vinokur (1957) with leaves of lemon trees and Fujiwara and Suzuki (1961) with barley, that translocation is drastically reduced by low soil temperature, and enhanced at higher soil temperatures. The results of this study conform with the findings of these researchers.

Wardlaw (1968) in his review of the control and pattern of movement of carbohydrates in plants pointed out there is little indication in most work whether the optimal temperature for translocation ever differs from that for growth. Although the present results support this view, certain exceptions were noted. Poor root growth at a high air and soil temperature (25°/15°C, 35°C), for example, occurred where the rate of photosynthesis and translocation to the roots was high. An accumulation of photosynthates to the roots clearly took place but there was apparently some inability to use them for growth. Rates of respiration of plants increase with increasing air and soil temperature (Kramer, 1962; Pharis, 1966; Rook, 1969c; Cooper, 1973; Rook and Hobbs, 1975; Abod, 1977) and large amounts of photosynthate can be lost from the plant through respiration (Baker, 1950; Moller, 1954; Kozlowski and Winget, 1964; Kozlowski and Gentile, 1968; Gordon and Larson, 1968; Ursino *et al.*, 1968). Respiration of the meristematic region of elongating root tips of trees is higher than most other tissues (Kramer and Kozlowski, 1960). The one particular

result noted above was quite conceivably the result of excessive respiration in the root zone at soil temperatures as high as 35°C. A number of other results at the higher soil temperatures of 30°C and above under the highest air temperature were no doubt influenced in a similar way.

The increased ^{14}C content of roots at the low air temperature and in the new root tips of seedlings at low soil but warm air temperatures is evidence that utilization of photosynthates through respiration was retarded at low temperature, a metabolic process now widely recognized (e.g. Kramer, 1940; Negisi, 1966).

The active shoot growth of seedlings at the high air and soil temperature indicates there was competition between the root and shoot for available photosynthates. Large numbers of branches (*c.* 12) actively growing on seedlings at this temperature resulted in the greater proportion of photosynthates being accumulated in the branches of seedlings, leaving less material available for root growth.

The relatively small proportion of ^{14}C-photosynthates found in the roots under higher air temperature should be viewed cautiously in relation to other temperatures. There is some evidence that after long periods of photoassimilation, decreased ^{14}C content could be due to losses from the roots through respiration, root exudation or through redistribution of current photosynthates from the roots to the rest of the plant (Pristupa and Kursanov,1957; Ursino *et al.*, 1968). This emphasizes the fact that any analysis of total ^{14}C in the root after long periods of time following $^{14}CO_2$ assimilation reveal only net translocation. Perhaps one of the greatest problems in this kind of study is attempting to assess the magnitude of total ^{14}C-photosynthate translocated to the root, as differences in rates of respiration occur not only with different plant tissues but with different temperature treatments.

A most striking result of the translocation study was the far greater proportion of ^{14}C-photosynthate translocated to the roots of intact seedlings in comparison to root-pruned seedlings. For active root growth to get under way not only must photosynthesis be restored but also normal translocation rates of photosynthates must be restored. Only about half of what could be interpreted as normal translocation of photosynthates to roots in intact seedlings took place in root-pruned seedlings during the three week observation period. Reduced meristematic activity in these *P. radiata* seedlings must be one if,

not the major cause of the reduced translocation. It is known that roots exert an influence on the translocation process, acting as acceptors of assimilates (Nelson and Gorham, 1959; Starck, 1964; Shiroya *et al.*, 1968) and that the translocation of photosynthates to the root is much affected by the weight of the roots present (Nelson and Gorham, 1957; Nelson, 1962). Excision of roots and poor root development have been shown to cause a decrease in the accumulation of labelled photosynthates in the roots, a similar response to that observed in this study. The distribution pattern of assimilates after root-pruning, however, might have been altered due to other factors such as reduced photosynthesis, possible leakage of radioactive substances after root-pruning or more directly by the effect of water stress on the conduction of assimilates (Starck, 1964; Wardlaw, 1968).

Very significant needle desiccation and lower relative water contents of needles in root-pruned seedlings especially under warm air temperatures indicated seedlings were under some moisture stress. There is ample evidence that under such moisture stress there is a reduction in the rate of movement of assimilates out of the photosynthetic tissue, this question is well reviewed by Wardlaw (1968).

As needle desiccation was evident three days after root-pruning the amount of desiccation measured would be a reflection of this initial disruption of seedling moisture status rather than that of the plant at harvest. The differences in needle desiccation observed possibly reflect the actual imbalance between absorption and transpiration rates of seedlings under the various temperature regimes. Alternatively, these differences might have been the result of plant recovery under various temperature regimes following pruning. Within the optimum temperature range shoot growth and needle elongation are greater, consequently, at the end of three weeks when needle desiccation was measured the values obtained would reflect this increased growth. Results in a later study support this hypothesis.

A combination of low soil temperature and higher air temperatures ($20^{o}/10^{o}C$ - $30^{o}/20^{o}C$), resulted in the heaviest needle desiccation and lowest relative water content of needles. Water uptake is reduced at low soil temperatures (Kramer, 1940; 1942; 1956; Cameron, 1941; Ashby, 1960; Kuiper, 1964, 1972; Cooper, 1973; Kaufmann, 1975, 1977) and plants from a warm environment show a greater reduction in water uptake due to low soil temperature than plants grown under cooler conditions (Kramer, 1942, 1956; Kozlowski, 1943; Kuiper, 1964). Such

reduced water uptake would consequently result in reduction in leaf water potential and a leaf water deficit as observed in this study. Furthermore, many authors for example, Kriedemann (1971), Hinckley and Richie (1973), Mederski *et al.* (1975), Turner and Jarvis (1975) and Khairi and Hall (1976) indicate that water deficits in the plants cause stomatal closure and this leads to reduced photosynthesis. The reduced rates of photosynthesis, translocation and poor root growth observed at low soil temperatures under the $15^{o}/5^{o}C$, $20^{o}/10^{o}C$ and $25^{o}/15^{o}C$ air temperature regimes are most likely a function of this reduced water status.

Within the range of soil temperatures from $20^{o}C$ to $30^{o}C$ root-pruned seedlings had the lowest needle desiccation and both root-pruned and intact seedlings maintained relatively high needle turgidities. Also within this range the rates of photosynthesis, translocation of photosynthates to the roots, root regeneration potential and shoot growth were optimal.

It is not known at this stage how root-pruning *per se* affects the various physiological processes. Differences in moisture status of most seedlings as time progressed does indicate some changes were occurring. Work by van Dorsser (1969a, Rook (1969a,b, 1971) and van Dorsser and Rook (1972) has indeed shown that physiological adjustments do occur in *P. radiata* seedlings when root systems are disturbed by wrenching. This question is further explored in the next chapter.

CHAPTER 9

AN EXAMINATION OF THE PHYSIOLOGICAL RECOVERY OF SEEDLINGS IN THE PERIOD IMMEDIATELY FOLLOWING ROOT-PRUNING

9.1 INTRODUCTION

It has now been shown that shoot growth and root-regeneration potential of root-pruned seedlings of *P. radiata* respond differently to variations in some environmental factors. In all of these studies the effects were assessed three to four weeks after the seedlings were root-pruned. A number of questions can be posed, for example:

a) what are the immediate effects of root-pruning on the physiological processes of the seedlings?

b) given a certain set of environmental conditions how long does it take for seedlings to recover from the initial shock of root-pruning?

c) what are the physiological processes most effected by the pruning treatment?

This final section of the study was carried out to explore these questions. The experiment was conducted over a thirty-two day period following root-pruning, at which time a number of physiological processes such as photosynthesis, respiration, stomatal behaviour and water relations were examined under favourable environmental conditions.

9.2 MATERIALS AND METHODS

Eighty seedlings (seed origin: Yarralumla, A.C.T.) were raised at CERES phytotron in an open glasshouse run at a 21^{o}C day and 16^{o}C night temperature. When 157 days old, forty-four seedlings were carefully selected for uniformity in size, and root-pruned (for details see Chapter 3). Root systems were pruned to 21 cm from the cotyledons and any remaining white root tips were pinched off. The pruning was completed over a period of two days. After being root-pruned each seedling was repotted, the shoot secured with a stake and the pots were returned to the glasshouse. At this time, seedlings were divided into groups assigned to various harvest dates.

The growth response of root-pruned seedlings was measured at intervals over a thirty-two day period. Seven harvests were made. The harvest dates and the number of seedlings harvested are presented in Table 9.1. The diameter and height measurements of seedlings assigned to each harvest are included in the table and illustrate the uniformity of the experimental material available.

Table 9.1 Harvest dates and number of seedlings harvested. The mean initial diameter and height of seedlings at each harvest are presented.

Harvest date (days after root-pruning)	Number of seedlings harvested	Initial diameter (mm)	Initial height (cm)
8	8	7.91	38.60
12	4	7.11	36.50
16	8	7.77	34.88
20	4	7.07	37.40
24	8	7.87	37.60
28	4	7.19	37.30
32	8	7.90	36.74

During the study the following observations were made:

a) Root Regeneration Potential and Shoot Growth

Root regeneration potential for each seedling included in the harvest was determined on the basis of the numbers of new white roots ≥ 0.1 cm (GT), ≥ 1.5 cm (LR), 0.1-1.4 cm (SR) and the total (TL) and average (AL) lengths of all new roots. Diameter and height were measured; increment, relative rates of diameter and height growth were calculated; the final dry weight of shoot, regenerated root and total root and root:shoot ratio were determined.

b) Water Potential of Seedlings

Leaf and xylem water potential were measured with a pressure bomb in the manner described by Scholander *et al.* (1965), Pierpoint (1967), Waring and Cleary (1967). Leaf water potential was measured

on intact seedlings and then at 1, 2, 5, 8, 16 and 20 days after root-pruning. Xylem water potential was measured on intact seedlings and at each harvest. Needles only were used in determining the water status during the first days after root-pruning as the pressure bomb technique requires destructive sampling of whole seedlings. Measurements were made on single needle fascicles selected at mid-height of randomly chosen seedlings. Six determinations were made at each measurement time.

At each harvest, whole seedlings were used for xylem water potential estimations. Only the upper 20 cm of stem could be included in the bomb. Five replicates were taken at 8, 16, 24 and 32 days after root-pruning, four replicates only at 12, 20 and 28 days after root-pruning.

c) Relative Turgidity

The relative turgidity (relative water content of needles) was determined at each harvest using the same procedure and formula as described in Chapter 8 (Section 8.4.1.2). For each determination, six fascicular needles were selected at mid-height from randomly chosen seedlings. All dried needle tips were excluded from the weight measurements.

d) Per cent Needle Desiccation

Total needle desiccation was determined from four seedlings at each harvest, using the method described in Chapter 8 (Section 8.4.1.1).

e) Stomatal Resistance

The response of stomatal resistance (aperture) to root-pruning over time was measured with a ventillated diffusion porometer (Turner and Parlange, 1970; Waggoner and Turner, 1971). The porometer registers the vapour diffusion from the needle surface, thus, the resistance measured is a combination of the stomatal and cuticular resistances. But, since most of the diffusion occurs through the stomatal pores, the resistance will be referred to as stomatal resistance.

Ten, three-needled fascicles were used in the determinations of stomatal resistance for intact seedlings and for seedlings 1, 2, 5, 8, 12, 16 and 20 days after root-pruning. Needles were chosen at mid-height of seedlings. For each measurement, each fascicle was inserted 3.5 cm into the acrylic chamber of the porometer. Any desiccated needle tips were removed prior to measurement. The cut end was dipped into petroleum jelly to prevent excessive water loss. Estimations of the volumes of the needle portions used in the measurements were made using a volumetric cyclinder. Needle area was determined from the volumes measured, as described by Wood (1969, 1971) for *P. radiata*.

f) Rates of Transpiration of Excised Needles

Rates of stomatal and cuticular transpiration of excised needles were measured on intact seedlings and seedlings at 8, 16, 24 and 32 days after root-pruning. Determinations were made gravimetrically (Jarvis and Jarvis, 1963; Bannister, 1964).

Fascicular needles were removed from mid-height of the seedlings, placed with their cut ends in water in sealed test-tubes and left for 24 hours under low light to attain full turgidity. By beginning at full water saturation, the method eliminates any non-specific effect of water balance (temporary daily or permanent water deficit, hydroactive closing of stomata), so that different plants are compared under the same conditions (Slavik, 1974). The needles were removed from the test-tubes, the desiccated tips removed if any, dried quickly with absorbent tissue and weighed on a torsion balance. This weight was taken as the saturated weight. The needles were then placed side by side on a sarlon cloth support frame, in a growth cabinet maintained at approximately $25^{o} \pm 0.5^{o}C$ temperature, 55 ± 2% relative humidity and $572 \mu Em^{-2}sec^{-1}$ (2700 f.c.) light intensity. Needles were allowed to transpire over a period of 240 minutes - being weighed periodically on a torsion balance. Weighings were made at ten minute intervals at the start and gradually reduced in frequency towards the end of the experiment.

Six determinations were made at each measurement time. At the end of the experiment, the needles were oven-dried and their dry weight determined so that the change in relative turgidity (relative water content) with time could be plotted. Relative turgidity was calculated as previously described in Chapter 8 (Section 8.4.1.2).

The technique also gives reliable estimates of the relative turgidity at which stomatal closure occurs. However, because of the difficulty in determining stomatal closure precisely and quantitatively from a simple plot of relative turgidity and time, an arbitrary point in the closing phase was determined by extrapolating to their intersection the straight line portions of a semi-logarithmic plot of changing relative turgidity with time (Jarvis and Jarvis, 1963). Such intersections were determined for each needle, thus making a quantitative comparison possible.

g) Rates of Net Photosynthesis and Dark Respiration

The rate of photosynthesis and dark respiration was measured for three seedlings at each harvest. The values were expressed in terms of green and total needle dry weight. In addition, photosynthesis and respiration of three seedlings was measured prior to root-pruning and thereafter on the first, second, fifth and eighth day after root-pruning. Net photosynthesis and respiration were calculated as $mgCO_2$/g/hr (see Chapter 3, section 3.5.1.1) on the basis of total dry weight of needles at day 8. This dry weight was used in calculating gas exchange rates at day 1 to 5 assuming that the change in dry weight during the eight days was negligible.

All gas exchange measurements were made by infra-red gas analysis as detailed in Chapter 3 (section 3.2.3), from 1100 to 1400 hours and at least $1\text{-}1\frac{1}{2}$ hours after thorough watering. Net photosynthesis measurement took place at a temperature of $21^{o}C$ under a light intensity of approximately $735\mu Em^{-2}sec^{-1}$ (3500 f.c.). After measurement each seedling was placed into a darkened LBH growth cabinet run at $16^{o}C$. When all photosynthesis measurements were complete, dark respiration was then measured for each seedling at a temperature of $16^{o}C$.

Because the seedlings were quite tall (c .37 cm) it was not possible to include the entire shoot in the assimilation chamber. Only the terminal 20 cm was used in gas exchange determination. A 4 to 5 cm segment of stem was cleaned of needles immediately below the 20 cm point and the stem rubbed with petroleum jelly to prevent any possible water loss. This allowed seedlings to be set up and removed from the assimilation chamber rapidly, with minimal damage to the rest of the stem and needles.

9.3 RESULTS

9.3.1 Statistical Analysis

Differences in the various parameters between measurement times were compared using Duncan's multiple range test at the 5% level of significance.

9.3.2 Root Regeneration Potential and Shoot Growth

The root regeneration potential and shoot growth measured at each harvest are presented in Table 9.2. The numbers (GT, LR, SR) and lengths (TL, AL) of new roots produced by seedlings increased with time (Figure 9.1). The rate of production of new roots was quite low until day 20, but, thereafter, the numbers of new roots within the various categories increased at an ever increasing rate with time.

Diameter and height growth were both suppressed for the first eight days after root-pruning. Diameter growth remained low until the sixteenth day and then some growth continued, probably at a fairly even rate allowing for experimental sampling error, through to the thirty-second day. In contrast, height growth picked up markedly at the end of eight days and continued at a fairly steady rate through to the end of the observation period of thirty-two days.

As was expected, there was a tendency for the final dry weight of the seedling's shoot, regenerated root and total root to increase with time. Root:shoot ratios showed little change with time, as also might be expected over such a short period.

9.3.3 Plant Moisture Status

The changes in xylem and leaf water potential of seedlings over time are presented in Table 9.3 and Figure 9.2. The values of xylem and leaf water potential both showed little difference in the moisture status of seedlings prior to root-pruning and some time after root-pruning (Figure 9.2). However, the leaf water potential measurements taken before day 8 decreased from the initial value of -9.27 bars in intact seedlings to -11.42 on the first day and -13.14 on the fifth day after which time the values returned to pre-pruning levels (Figure 9.2b).

Table 9.2 Root regeneration potential and shoot growth of seedlings measured over a thirty-two day period following root-pruning. Bracketed values represent the number of days after root-pruning.

Parameter	Treatment Means						
Root Regeneration							
Number of new roots ≥0.1cm (GT)	38* (8)	100 (12)	114* (16)	254 (20)	506 (28)	700* (24)	888* (32)
Number of new roots ≥1.5cm (LR)	1* (8)	2 (12)	14* (16)	123 (20)	155 (28)	233* (24)	410* (32)
Number of new roots 0.1-1.4 cm (SR)	37* (8)	98 (12)	100* (16)	131 (20)	351 (28)	467* (24)	478* (32)
Length of new roots ≥0.1cm (TL) in cm	20.76* (8)	55.32 (12)	90.71* (16)	449.88 (20)	876.90 (28)	1,069.35* (24)	1,831.80* (32)
Average length of new roots ≥0.1cm (AL)	0.52* (8)	0.59 (12)	0.59* (16)	1.45 (20)	1.47* (24)	1.78 (28)	1.99* (32)
Diameter and Height							
Initial diameter (mm)	7.07 (20)	7.11 (12)	7.19 (28)	7.77* (16)	7.87* (24)	7.90* (32)	7.91* (8)
Diameter increment (mm)	0.01 (12)	0.01* (8)	0.03* (16)	0.28* (24)	0.34 (28)	0.37 (20)	0.60* (32)
Relative growth rate of diameter ($mm.mm^{-1}.day^{-1}$)	0.0001 (12)	0.0001* (8)	0.0003* (16)	0.0015* (24)	0.0016 (28)	0.0023* (32)	0.0026 (20)
Initial height (cm)	34.88* (16)	36.50 (12)	36.74* (32)	37.30 (28)	37.40 (20)	37.60* (24)	38.60* (8)
Height increment (cm)	0.25* (8)	2.01* (16)	2.10 (12)	3.28 (20)	4.09* (24)	4.62* (32)	5.22 (28)
Relative growth rate of height ($cm.cm^{-1}.day^{-1}$)	0.0008* (8)	0.0034* (16)	0.0039* (32)	0.0040 (20)	0.0043* (24)	0.0045 (12)	0.0045 (28)
Final Dry Weight							
Shoot (g)	14.224 (12)	16.600* (8)	18.210 (20)	18.600* (16)	18.971 (28)	20.619* (24)	22.103* (32)

(Cont'd next page)

Table 9.2 (Cont'd)

Parameter	Treatment Means						
Regenerated root (g)	0.006* (8)	0.016 (12)	0.030* (16)	0.127 (20)	0.337 (28)	0.363* (24)	0.716* (32)
Total root (g)	4.034 (20)	4.151 (12)	4.620* (16)	4.738* (8)	5.332 (28)	5.400* (24)	6.200* (32)
Root:shoot ratio	0.23 (20)	0.25* (16)	0.27* (24)	0.28* (32)	0.29* (8)	0.29 (28)	0.30 (12)

* Mean of 8 replicates, other values mean of 4 replicates.

Note: Horizontal lines join means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

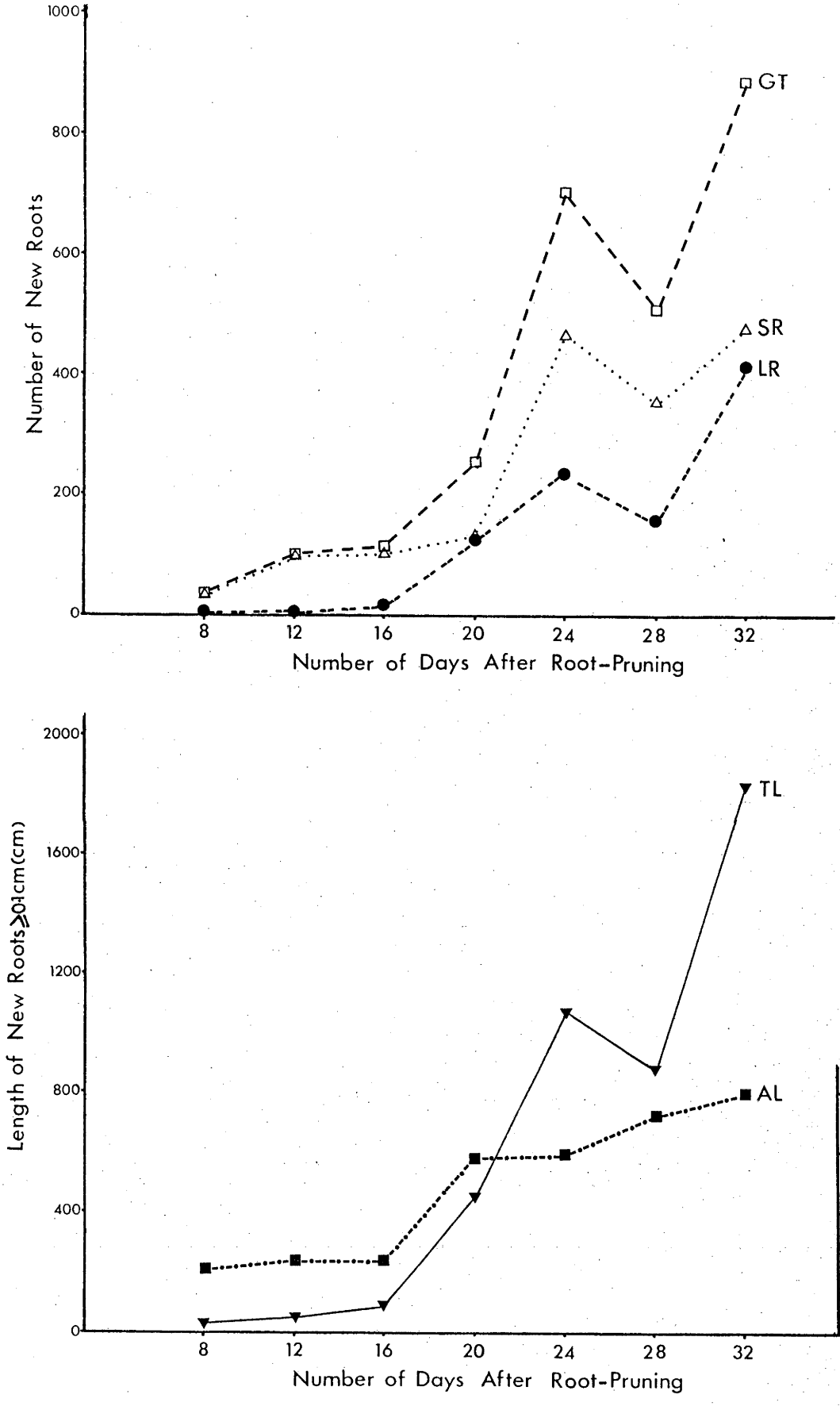

Figure 9.1. Root regeneration potential of *P. radiata* seedlings measured over a thirty-two day period after root-pruning. Values at day eight, sixteen, twenty-four and thirty-two are means of eight replicates. Other values are means of four replicates.

Table 9.3 The xylem and leaf water potential of seedlings over a period of thirty-two days following root-pruning. Bracketed values represent the number of days after root-pruning at which measurement was taken. 'I' represents measurement of intact seedlings prior to root-pruning.

Parameter	Treatment Mean[1]							
Xylem Water Potential (-bars)	6.01 (32)	7.26 (20)	7.48 (12)	7.60 (I)	7.62 (28)	7.66 (24)	7.69 (8)	8.87 (16)
Leaf Water Potential (-bars)	8.85 (20)	9.12 (8)	9.19 (12)	9.27 (I)	10.90 (2)	10.93 (16)	11.42 (1)	13.14 (5)

1 Mean of (a) 5 and 4 replicates for xylem water potential at I, 8, 16, 24, 32 and 12, 20, 28 days respectively.
(b) 6 replicates for leaf water potential.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

Table 9.4 Relative turgidity of needles measured over a thirty-two day period following root-pruning. Bracketed values represent the number of days after root-pruning at which measurement was taken. 'I' represents measurement of intact seedlings prior to root-pruning.

Relative Turgidity (%)[1]									
76.8 (24)	82.1 (12)	82.2 (2)	82.9 (20)	8.35 (32)	84.5 (8)	84.9 (1)	87.3 (I)	89.0 (5)	89.6 (28)

1 Each value the mean of 6 replicates.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

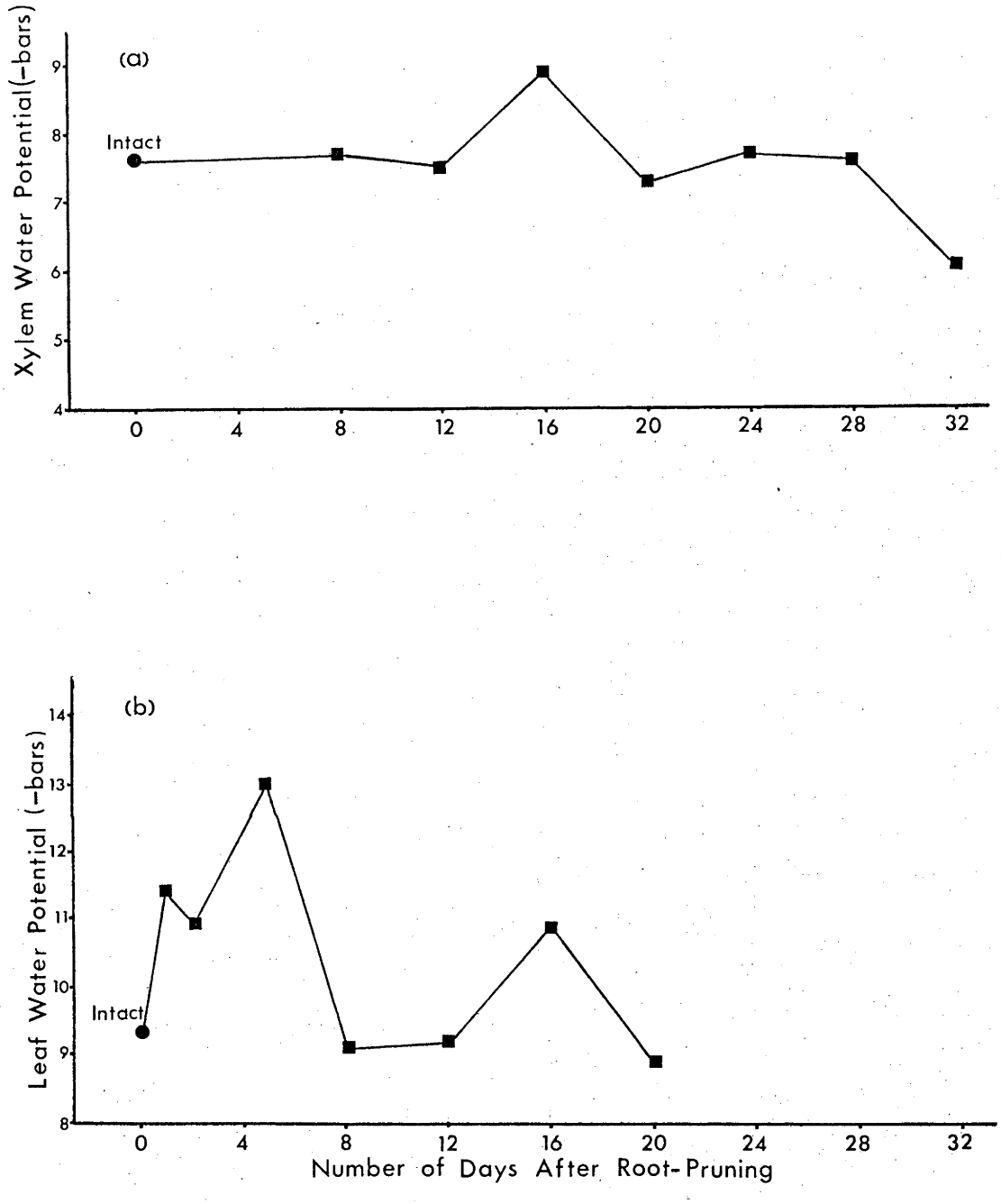

Figure 9.2. Xylem water potential (a) and leaf water potential (b) measured for *P. radiata* seedlings over a thirty-two day period following root-pruning.

As shown in Table 9.4 measurements of needle relative turgidity were somewhat erratic. The values ranged from 76.8% (day 24) to 89.8% (day 28). Relative turgidity showed no consistent trend with time.

Per cent total needle desiccation (Table 9.5) showed a tendency to decrease with time. The heavy loss of needles measured at day 8 is due to increased water stress immediately after root-pruning. Desiccation was evident three days after pruning. The decreasing proportion of desiccated needles suggests an increase in green needle weight due to needle elongation and shoot growth, rather than an actual decline in desiccation. This decrease in needle desiccation parallels an increase in the photosynthetic rates of seedlings, expressed in terms of total needle dry weight, after day 8.

Table 9.5 Per cent needle desiccation of seedlings measured from eight to thirty-two days following root-pruning.

Needle Desiccation (%)[1]						
23.9	29.7	29.7	35.9	43.4	48.2	57.3
(28)	(32)	(24)	(20)	(16)	(12)	(8)

1 Each value the mean of 4 replicates.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

9.3.4 Stomatal Resistance

After root-pruning the seedlings showed a sharp increase in stomatal resistance (Figure 9.3) with the highest value of 21.20 sec per cm recorded on day 8 (Table 9.6). After day 8 stomatal resistance decreased, but, there were no significant differences in stomatal opening from day 12 to 20 which remained at levels well above those of the intact seedlings.

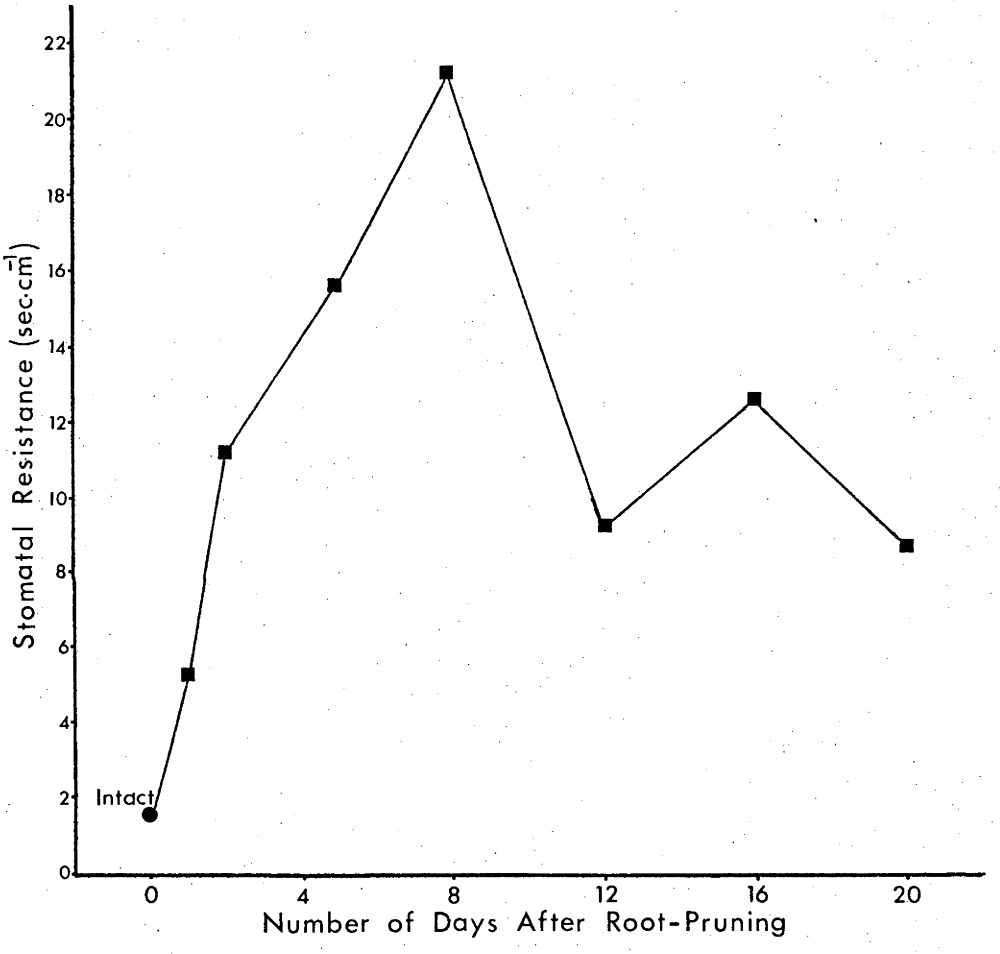

Figure 9.3. Stomatal resistance measured over a twenty day period following root-pruning.

Table 9.6 Stomatal resistance measured over a twenty day period following root-pruning. Bracketed values represent the number of days after root-pruning at which measurement was taken. 'I' represents measurement of intact seedlings prior to root-pruning.

Stomatal Resistance ($Sec.cm^{-1}$) [1]							
1.56	5.22	8.57	9.20	11.16	12.60	15.60	21.20
(I)	(1)	(20)	(12)	(2)	(16)	(5)	(8)

1 Each value the mean of 10 replicates.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

For the short time immediately after root-pruning (one to five days) marked increases in stomatal resistance were paralleled by marked decreases in leaf water potential. At day 8, while stomatal resistance reached its highest value, leaf water potential had returned to the same level as prior to root-pruning. It was apparent that from day 5 to day 8 leaf water potential recovered dramatically from the observed low value at day 5. The steady increasing stomatal resistance at this time suggests that stomatal closure was responsible for reduced moisture stress in seedlings. After day 8 stomatal resistance decreased and both leaf water potential and stomatal aperture were maintained at fairly constant levels for the remainder of the thirty-two day period.

9.3.5 Rates of Transpiration of Excised Needles

The decline in relative turgidity and transpiration rate of excised needles for intact seedlings and at 8, 16, 24 and 32 days after root-pruning are shown in Figure 9.4 and 9.5 respectively. All needles sampled showed a similar pattern of water loss irrespective of the day of sampling.

The initial rate of water loss was greatest in needles from intact seedlings and from seedlings 32 days after root-pruning

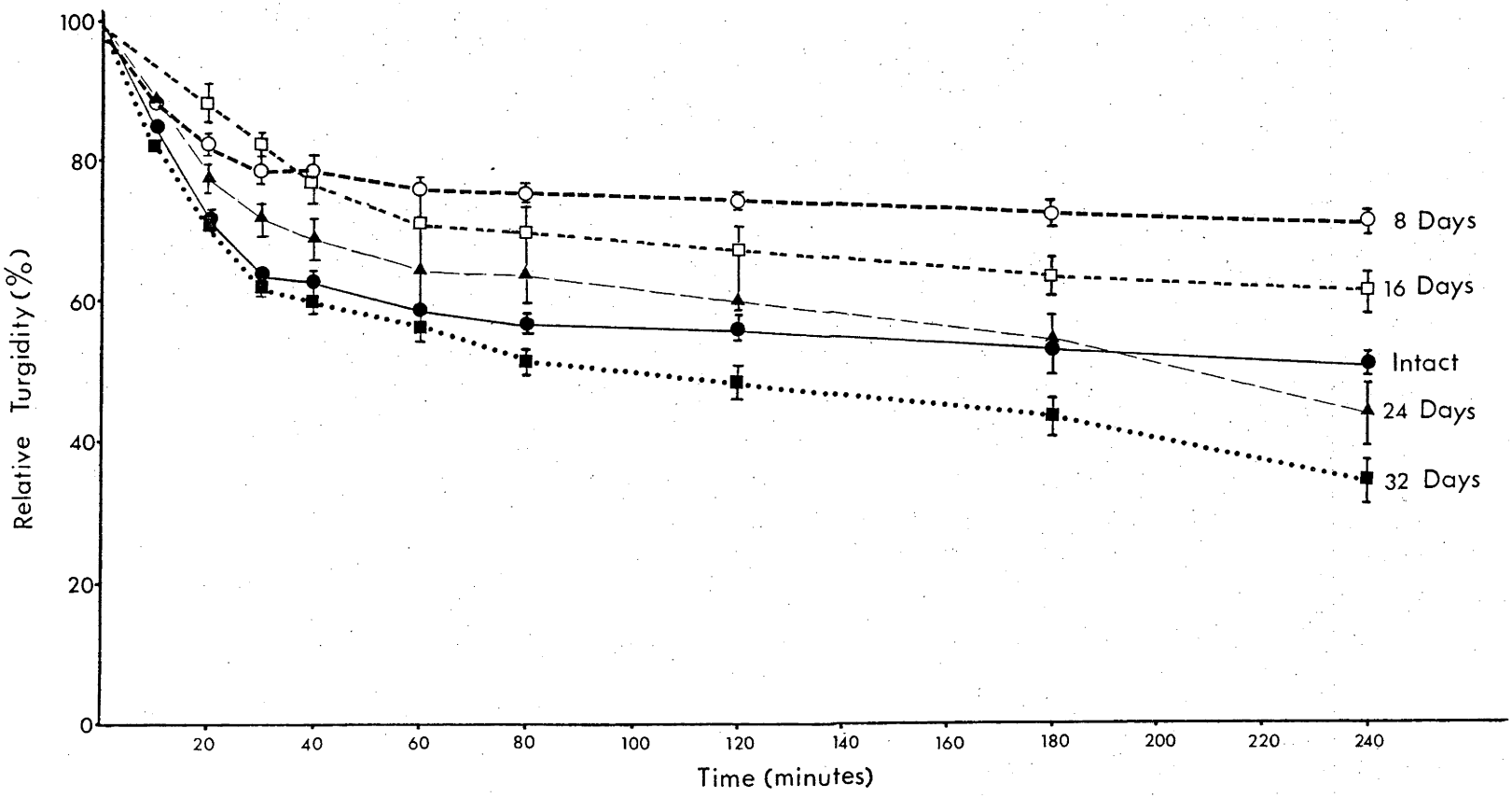

Figure 9.4. The decline in relative turgidity of excised needles of *P. radiata* with time, measured for intact seedlings and at eight, sixteen, twenty-four and thirty-two days after root-pruning. Each point represents a mean of six replicates. Vertical bars represent standard errors.

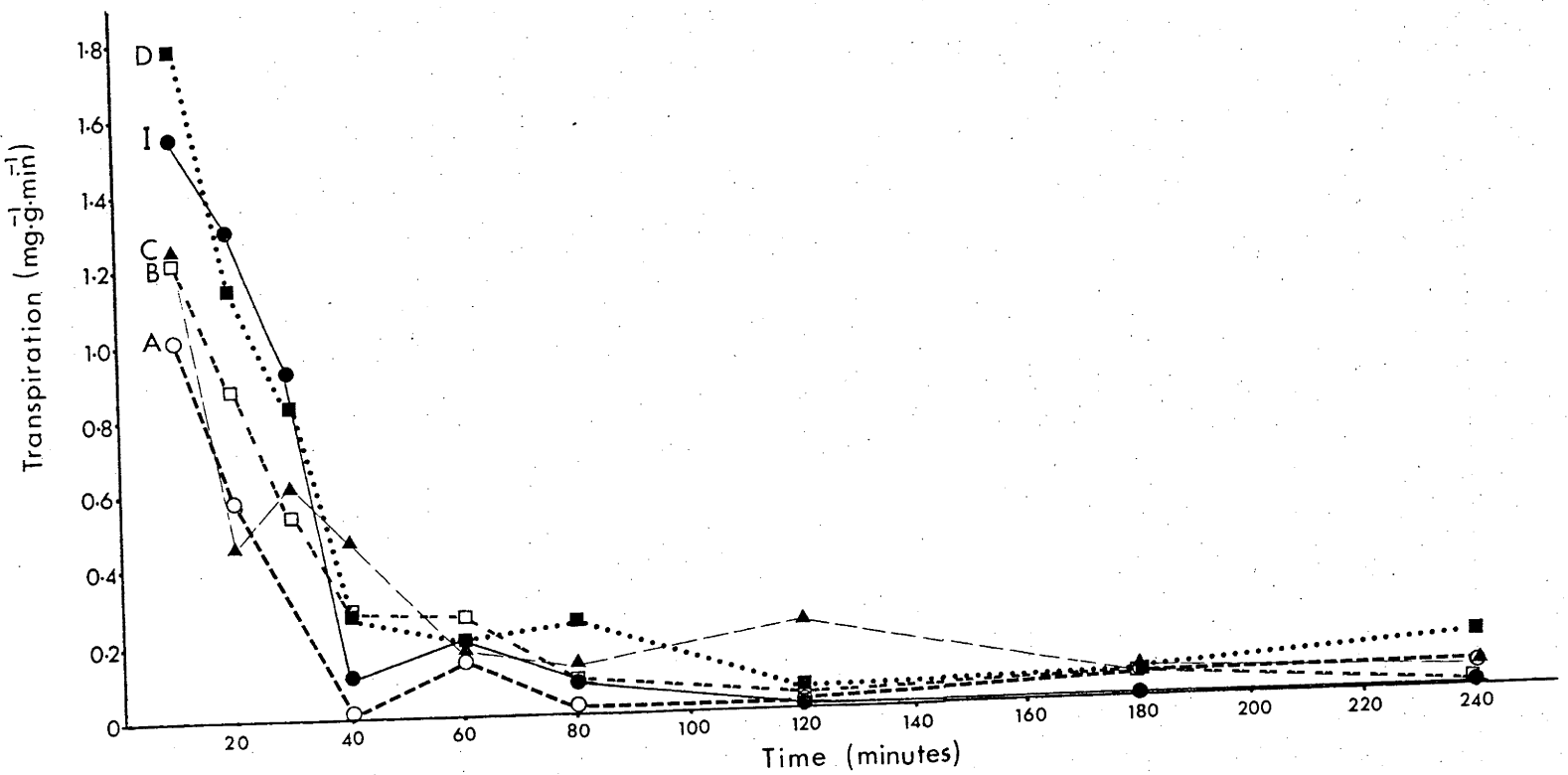

Figure 9.5. Transpiration rates of excised needles of *P. radiata* seedlings measured at eight (A), sixteen (B), twenty-four (C) and thirty-two (D) days after root-pruning and of the original intact seedlings (I). Each point represents a mean of six replicates.

(Figure 9.5). The initial rate of water loss was least from needles collected 8 days after root-pruning with 16 and 24 day treatments assuming intermediate positions.

After forty minutes the rate of water loss was considerably reduced in all of the material measured apparently from stomatal closure. By this time, the relative turgidity of needles of intact seedlings and those 32 days after root-pruning had declined(Figure 9.4) by approximately 38% and 40% respectively, while those measured at day 8 declined only 21%. The relative turigidies at which stomatal closure occurred was estimated by using a semi-logarithmic plot as described previously in section 9.2 (f). The closure relative turgidities are presented in Table 9.7.

Table 9.7 Needle relative turgidities at the point of stomatal closure. Bracketed values are the number of days after root-pruning at which time measurement was taken. 'I' represents measurement from intact seedlings.

Relative Turgidity (%)[1]				
59.33	59.33	66.33	72.00	78.50
(I)	(32)	(24)	(16)	(8)

1 Each value the mean of 6 replicates.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

Eight days after root-pruning seedlings showed the greatest sensitivity to reductions in relative turgidity. Stomatal closure occurred at a relative turgidity of 78.5% at this time, a closure value significantly higher than for the other treatments. These seedlings showed greater stomatal control of water loss. The stomata of intact seedlings and seedlings 32 days after root-pruning were much more ineffective and slower in closing compared to other seedling. Stomatal closure occurred when plant relative turgidities had declined to 59.33%.

9.3.6 Net Photosynthesis and Dark Respiration

Net photosynthesis and dark respiration where measured at various times after root-pruning (Table 9.8 and Figure 9.6). There was a sharp decline in photosynthesis during the first eight days after root-pruning followed by a very gradual recovery in photosynthesis to a level equal to about 60% of the original rate in intact seedlings expressed in terms of green needle dry weight or about 50% expressed in terms of total needle dry weight. Dark respiration increased immediately after root-pruning (day 1 and 2), then declined to a fairly constant level thereafter.

The decline in photosynthesis closely paralleled the increase in stomatal resistance for the first few days after root-pruning. After three days needle desiccation was evident indicating that stomatal closure alone was not responsible for the reduced gas exchange values after this time. The higher rates of photosynthesis and respiration when expressed in terms of green needle weight is evidence of this.

9.4 DISCUSSION

The results indicate that root-pruning had an immediate and marked effect on a number of physiological processes. These effects occurred within the first eight days following root-pruning.

The most striking effect observed was a sharp increase in stomatal resistance and a concurrent drop in net photosynthesis. A decline in photosynthesis due to root-pruning has also been reported for *Pinus caribaea* (Abod, 1977). A number of investigators have shown that increasing water deficits can cause an increase in stomatal resistance accompanied by a reduction in photosynthesis (e.g. Ketellaper, 1963; Boyer, 1965; Kriedemann, 1971; Mederski *et al.*, 1975; Khairi and Hall, 1976). The most tangible evidence of a reduced capacity to maintain water balance was the increased leaf water potential and observed needle desiccation which occurred within a few days of the root-pruning treatment. Since the seedlings were incapable of maintaining high rates of absorption due to a much reduced root system, the closure of stomata is the only means by which seedlings could exercise control over water loss. It was shown on excised needles, such that within the eighth day period stomata from

Table 9.8 Rates of net photosynthesis and dark respiration of seedlings measured over a thirty-two day period following root-pruning. Values are the means of three replicates. Bracketed values represent the number of days after root-pruning at which measurement was taken. 'I' represents measurement of intact seedlings prior to root-pruning.

a) Comparison of measurements from day 0 (intact) to day 8.

Parameter	Treatment Mean				
Net Photosynthesis[1] ($mg.g^{-1}.hr^{-1}$)	2.87 (8)	5.43 (5)	9.74 (2)	12.31 (1)	14.81 (I)
Dark Respiration[1] ($mg.g^{-1}.hr^{-1}$)	0.77 (8)	1.34 (5)	1.38 (I)	1.53 (2)	1.95 (1)

b) Comparison of measurements from day 0 (intact) to day 32.

Parameter	Treatment Mean										
Net Photosynthesis[1] ($mg.g^{-1}.hr^{-1}$)	2.87 (8)	4.71 (24)	4.95 (16)	5.28 (20)	5.43 (5)	6.43 (32)	6.70 (12)	6.89 (28)	9.74 (3)	12.31 (2)	14.81 (I)
Dark Respiration[1] ($mg.g^{-1}.hr^{-1}$)	0.77 (8)	0.88 (24)	0.93 (12)	0.97 (16)	0.99 (20)	1.17 (28)	1.34 (5)	1.35 (32)	1.38 (I)	1.53 (2)	1.95 (1)

c) Comparison of measurements from day 8 to day 32.

Parameter	Treatment Mean						
Net Photosynthesis[2] ($mg.g^{-1}.hr^{-1}$)	6.32 (8)	7.24 (20)	8.60 (16)	8.64 (12)	8.86 (28)	9.56 (32)	10.49 (24)
Dark Respiration[2] ($mg.g^{-1}.hr^{-1}$)	1.35 (32)	1.36 (20)	1.66 (12)	1.70 (16)	1.81 (24)	1.83 (28)	1.98 (8)

1 Gas exchange expressed in terms of total needle dry weight.

2 Gas exchange expressed in terms of green needle dry weight.

Note: Horizontal lines join means that are not significantly different at $P_{0.05}$ (Duncan's multiple range test).

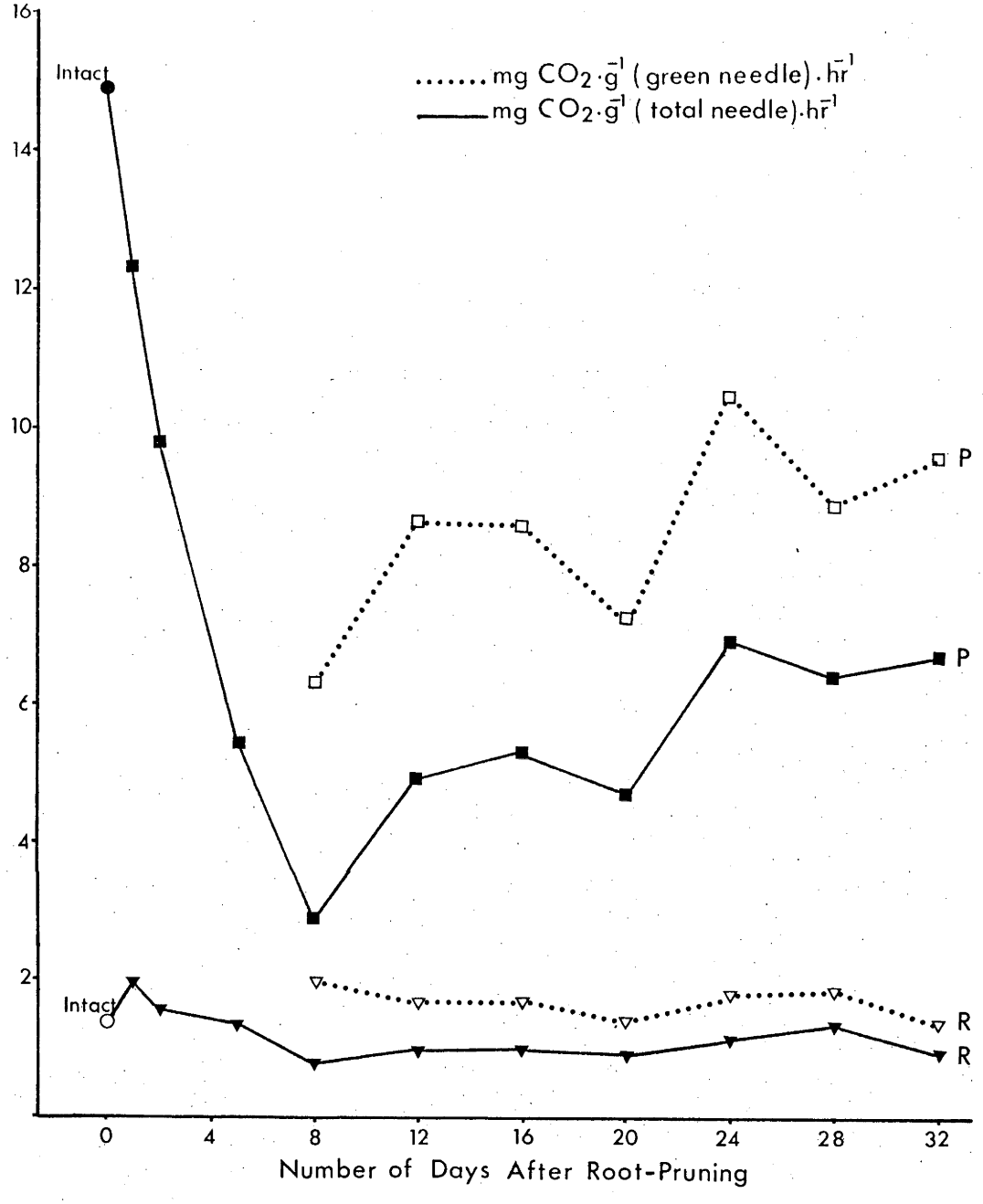

Figure 9.6. Rate of net photosynthesis (P) and dark respiration (R) of seedlings over a thirty-two day period following root-pruning.

root-pruned seedlings were more sensitive to water loss than were the stomata of needles from unpruned seedlings (Figure 9.5). Similar behaviour has been shown for *P. radiata* seedlings grown under moisture stress (Rook, 1973).

That seedlings undergo moisture stress within this period is further supported by the respiratory response. There was a tendency for dark respiration to increase immediately after root-pruning (day 1 and 2) after which time the rate declined to a level maintained consistently for the remainder of the thirty-two day period. Such behaviour has been shown for root-pruned *P. caribaea* seedlings (Abod, 1977) and a number of other plants under moisture stress (Stocker, 1960; Boyer, 1976).

An alternative explanation for the reduced rates of photosynthesis of seedlings is perhaps related to the temporary reduction in the size of the sink (roots) for photosynthates. More photosynthates would be expected to accumulate in the shoot, which in turn would reduce the rate of photosynthesis (e.g. review by Neales and Incoll, 1968).

Eight days after root-pruning leaf water potential was restored to pre-pruning level and by day 12 seedlings showed distinct signs of recovery in photosynthesis, accompanied by a decrease in stomatal resistance. Proliferation of new roots took place and thereafter, the recovery process intensified. By day 32 net photosynthesis was restored to approximately 60% (green needle weight) or 50% (total needle weight) of the initial rate prior to root-pruning. There was also less sensitivity in stomatal response to moisture loss (Figure 9.5). Associated with this recovery were progressive increases in both root regeneration and shoot growth.

Thus, it is apparent that root-pruning has a marked effect on the physiological processes of *P. radiata* seedlings. However, the seedlings have effective mechanisms to minimise the adverse effects of the initial shock of root-pruning ensuring both survival and subsequent growth given favourable conditions.

CHAPTER 10

GENERAL DISCUSSION

Successful seedling establishment in the forest depends on a combination of many environmental factors and the inherent, morphological and physiological capabilities of the seedling. The fundamental difference between the container grown seedling once outplanted and the conventional bare-rooted seedling is the greater root disturbance of the latter. Bare-rooted stock must rely more on the resources immediately available from the site after planting for survival and subsequent growth. Seedling capacity for rapid root growth and exploration of the soil immediately after planting is a critical factor in rapid establishment and fast growth during the first growing season.

P. radiata is one of the most successful conifers as an exotic in commercial plantations in the world. This success has been attributed to its hardy nature and a capacity for rapid growth under a wide range of environmental conditions (Shepherd, 1971; Waring, 1971). It is a species with the capacity to be planted bare-rooted into the forest yet to become established and to grow at an extremely fast rate during the following months (Woods, 1976). Many questions may be asked in relation to the underlying mechanisms contributing to these favourable characteristics, especially its capacity for bare-root planting. What physiological processes are involved in determining its success once outplanted? How does the environment effect its growth potential? The studies in this thesis set out to explore some of these questions of particular relevance to the question of root growth both during the critical establishment phase and following the practice of undercutting and wrenching in the nursery, a practice known to result in a hardened plant with a fibrous root system particularly well suited to field planting (Cameron, 1969; Cameron and Rook, 1969b; Rook, 1969a, 1971; van Dorsser and Rook, 1972; Benson, 1976a,b; Benson and Shepherd, 1977; Chavasse, 1977).

Root regeneration potential (RRP), the capacity of seedlings to produce new roots has been shown to be one of the most critical indicators of the physiological condition of seedlings (Schubert and Adams, 1971; Stone and Jenkinson, 1971). Stone and his co-workers and many other researchers have successfully used this technique in predicting the transplanting capacity of a number of nursery conifers including *P. ponderosa* (Stone and Schubert, 1958, 1959a,b; Schubert and Baron, 1965; Stone, 1967a; Stone and Jenkinson, 1971), *P. taeda* (Bilan, 1961), *Ps. menziesii* (Stone, 1955; Stone *et al.*, 1962; Todd, 1964), *Taxus* spp. (Lathrop and Mecklenburg, 1971) *P. glauca*, *P. mariana* and *P. banksiana* (Stupendick, 1973; Day and Stupendick, 1974; Day and MacGillivray, 1975; Day, Stupendick and Butler, 1976). All have found that there was an endogenous seasonal rhythm to this capacity for root regeneration, the seasonal patterns varying with species. Nursery grown *P. ponderosa* and *Ps. menziesii*, for example, lifted in late spring and summer have little capacity for root regeneration but lifted in late autumn or winter have a high capacity for root regeneration. These researchers found that certain environmental factors such as air and soil temperature, light intensity, photoperiod and soil moisture were critical in determining the potential root growth of seedlings of these particular species on the planting site.

The present studies set out to investigate for *P. radiata* some environmental factors shown in the literature to influence RRP and which could be isolated singly in phytotron and glasshouse facilities so that the main effects of the single environmental factor could be revealed.

Shoot- and root-pruning, including undercutting and wrenching, are common cultural practices in *P. radiata* nurseries to regulate seedling size and as a preconditioning method to improve stock quality (Anon., 1968; Cameron and Rook, 1969b; van Dorsser and Rook, 1972; Stockley, 1975; Benson, 1976a; Minko and Craig, 1976). In undercutting and wrenching it is desirable to sever a significant proportion of the root system thereby severely stressing the seedling, then allowing recovery in the bed before lifting and outplanting.

Some early investigations in the present study set out to determine how much shoot and root could be removed from *P. radiata* seedlings before growth was too drastically reduced or mortality occurred. It was found that when the root system was reduced such that

no fibrous roots remained whatever, given favourable environmental conditions seedlings still possessed a phenomenal capability to survive and, in the long run, to proliferate a new root system. The results clearly showed, however, that most rapid root growth occurred when the least amount of root or shoot was removed. Under unfavourable environmental conditions, severely pruned seedlings could not be expected to develop new roots rapidly. Thus, unable to gain intimate contact with the soil for moisture and nutrient reserves, seedlings would, in the long term, die. Seedlings with some fibrous roots were found to be better able to establish than those with only rudimentary root systems. For the purposes of subsequent studies it was found that if 21 cm of root measured from the cotyledons remained this allowed for adequate root regeneration in the three to four week period following root-pruning, during which the effect of various environmental factors on seedling growth could be tested. The test period and the amount of root removed was a compromise situation as the process of counting and measuring the masses of new roots was very time-consuming and had to be balanced against the usefulness of the results obtained.

The effect of the nutritional status of seedlings during the critical period immediately after root-pruning was investigated. It was found that under such treatment seedlings which had been supplied with adequate nutrients throughout the growth period prior to root-pruning had sufficient reserves to sustain growth while new roots were produced. Plants grown under inadequate nutrient regimes showed poorer growth once root-pruned and replanted. In the present studies, regular nutrient applications both prior to and during treatment ensured that seedlings had sufficient nutrient reserves for the three to four week growth period after root-pruning. This certainly was so under the more favourable temperature conditions but, as noted elsewhere, nutrient uptake may have been limited during the treatment period at low soil temperatures. Chlorosis was evident in seedlings grown under a temperature regime of $8^{o}/4^{o}C$ (Chapter 7, Expt. 2), suggesting that nutrient deficiency may have been, in part, responsible for poor root growth at that temperature. There is very good evidence in the literature that low soil temperatures can restrict both uptake of nutrients from the soil and mobilization of nutrients in the plants (Vinokur, 1957; Ashby, 1960; Power *et al.*, 1963; Bowen, 1970 and

others cited by Knoll *et al.*, 1964 and Cooper, 1973). The results of the present study were thus shown, in general, not to be complicated by poor nutritional status of the seedlings, except, under low soil temperatures.

Knowing light intensity and photoperiod to be critical factors influencing the growth of seedlings, some early studies dealt with these environmental factors. In the Australasian environment where *P. radiata* is grown the average day-length varies only between about 9 and 15 hours (for Brisbane 28°S, 10.3-13.9 hrs; Sydney 34°S, 9.8-14.4 hrs; Melbourne 38°S, 9.5-14.7 hrs; and Hobart 43°S, 8.9-15.3 hrs). It was shown that within this range, seedlings have a high potential for root growth. Although shoot extension is favoured under longer days, photoperiod was shown not to be a critical factor influencing the RRP of seedlings. The light intensity experiment, however, did show that *P. radiata* was sensitive to reduced light levels. Both the size of the seedlings produced and RRP were affected by low light intensity. The normal, unshaded conditions when seedlings are planted into the field are therefore conducive to production of good root systems and sturdy plants. Under shade, seedlings develop poor root systems with slender, soft stems. The results confirm that current nursery practice for *P. radiata*, where no shade is used, is most favourable for the development of sturdy seedlings with well-developed root systems.

Temperature is one of the most important environmental variables regulating seedling growth and RRP (Bilan, 1961; Schubert and Baron, 1965; Krugman and Stone, 1966; Stone, 1966; Schubert and Adams, 1971; Stone and Jenkinson, 1971; Abod, 1977). In the present studies a wide range of ambient temperatures was examined, covering the range which would usually be experienced during the year under normal field conditions in Australasia. In early studies, where there was no separate control of soil temperature, it was found that RRP was extraordinarily high under a wide range of temperature regimes. Even at temperatures as low as 8°/4°C seedlings proliferated new roots. The distribution of root growth, however, differed under lower when compared to higher temperature regimes. While seedlings still produced large numbers of new roots at low temperatures, the subsequent extension of these roots was greatly reduced. None of the temperature regimes in these early studies completely inhibited growth.

In agreement with other studies with *P. radiata*, seedling growth and RRP were optimal at temperatures ranging from 21°/16°C to 27°/22°C (Shepherd, 1965; Cremer, 1968; Florence and Malajczuk, 1970; Macpherson, 1970; Hellmers and Rook, 1973; Wood and Brittain, 1973). Where the day and night differential was altered under a favourable 27°C day temperature the greater length of roots was produced at night temperature closest to the day temperature (22°C). A cold night (10°C) temperature altered the distribution of growth in the test seedlings. Height growth was enhanced while extension of many new roots produced was inhibited.

In all the early day/night temperature studies, soil temperature followed the air temperature within approximately half an hour of the day/night, night/day changeover. Consequently, it was not possible to differentiate between any separate effects of soil and air temperature. A perusal of the literature had shown that soil temperature was certainly likely to be a critical factor determining both seedling development (e.g. Barney, 1951; Ashby, 1960; Hellmers, 1963b; Bowen, 1970; Cooper, 1973; Heninger, 1974; Heninger and White, 1974; Rook and Hobbs, 1975) and RRP (Stone *et al.*, 1962; Schubert and Baron, 1965; Larson, 1970; Abod, 1977). This led to further studies which set out to examine the relative significance of soil temperature in relation to root regeneration potential.

Soil units were installed in the cabinets so that soil temperature could be controlled independently of a range of shoot temperatures.

Under all of the air temperature regimes examined, ranging from a low 15°/5°C to a high 30°/20°C, low soil temperatures (5°-10°C) were adverse to root regeneration potential. Under these conditions needle turgidity, photosynthesis and translocation of photosynthates to the roots were all reduced in root-pruned seedlings. Only relatively few roots were produced at these low temperatures, and almost all of these were short roots.

In Australia, cold soil temperatures of the same order as the experimental temperatures used, could be expected in the winter and early spring in the field or nursery (Jacobs and Lindsay, 1929; Bowen, 1970). Cold soils would depress root growth, thus seriously restricting exploration of the soil and the uptake of moisture (see Kuiper, 1964) or mineral nutrients (Bowen, 1970).

Low nutrient availability and especially paucity of P and N has long been recognized as a problem limiting growth in *P. radiata* nurseries and in the plantations (Brown and Hall, 1968; Waring, 1971; Benson, 1976a,b). There is evidence that nutrient deficiency may be one of the primary factors responsible for productivity decline in second rotation stands (Stevens and Bond, 1957; Lewis and Harding, 1963; Stone and Will, 1965a; Bednall, 1968; Whyte *et al.*, 1969; Berg, 1975), and that it does become a limiting factor even on the most fertile soils in nurseries after repeated cropping (Benson, 1976a; Minko and Craig, 1976). It is common practice to supply seedlings with fertilizer at the time of planting to the forest (e.g. Brown and Hall, 1968; Shepherd, 1971) and at seedbed preparation and regularly throughout the growing season in the nursery (Benson,1976b; Minko and Craig, 1976) to compensate for these nutrient deficiencies. Application of fertilizer at a time when cold soils would restrict root growth is not a useful practice as seedlings would be limited in their ability to take up any significant quantities of nutrient elements. Rapid leaching of nitrogenous fertilizers particularly is likely to take place under the wet conditions of winter. This could lead to much reduced availability of this fertilizer element in the proximity of the root zone when soils begin to warm up and root extension commences.

The highest soil temperatures examined were above the ambient air temperatures and when above 30°C would be comparable to very high temperatures only encountered in the field in the hottest summer months. At soil temperatures of 30°C and 35°C seedlings maintained relatively high rates of photosynthesis and translocated large proportions of photosynthate to the roots. Seedlings, however, grew preferentially in height and produced few roots and it was argued that excessive respiration was most probably the main cause of this. Complete inhibition of root growth and reduced photosynthetic rates of seedlings at the 40°C soil temperature indicates a gross disruption of the internal physiological processes of the seedlings.

Active shoot growth of intact seedlings at high soil temperatures suggested that the seedlings were extending roots rapidly. Careful observation of both root-pruned and intact root systems showed that the roots were fully suberized and apparently no new roots were being produced. One possible explanation was that suberization of roots was proceeding at the same rate as new root extension and the new

roots were thus brown and not readily recognized. However, the complete absence of new root tips and heavy suberization of the whole system tended to contradict such an hypothesis. Survival of most seedlings at this soil temperature indicated that plants were, however, quite capable of obtaining sufficient water through suberized roots. Although needle turgidity of root-pruned seedlings was low at these temperatures, intact seedlings maintained their moisture status at high levels. In the literature, reports by Addoms (1946), Kramer (1946), Kramer and Bullock (1966) and Chung and Kramer (1975) have indicated that suberized roots do in fact play an important role in the water economy and mineral nutrition of woody plants.

RRP was high at medium soil temperatures under each air temperature regime. The greatest potential to regenerate roots was found when soil temperature was similar to the air temperature. In general, root regeneration potential was high within a soil temperature range of 20°C to 30°C. In terms of daily heat sum of the soil, in both soil temperature controlled and uncontrolled experiments, there was a consistent occurrence of maximum root growth at 480 to 720 degree-hours. It is suggested that soil daily heat sum may be a critical factor influencing root growth of *P. radiata*. Within the optimal temperature range, seedling moisture status was most favourable, seedlings had high rates of photosynthesis and a high proportion of photosynthates were translocated to the roots.

Under the low air temperature regime of 15°/5°C height growth of both intact and root-pruned seedlings declined and diameter growth was enhanced. At the highest soil temperatures photosynthesis was adequate, needle turgidity high, with adequate distribution of photosynthates to both the stem and root. Very large numbers of new root were produced and although the warmer soils enhanced the extension of roots, a large proportion were still quite short. Certain implications for nursery practice may be inferred from these results. Undercutting and wrenching commenced in summer, for example, under conditions of adequate moisture and nutrient supply, would result in a quite active proliferation of roots together with shoot extension. As autumn progresses air temperatures decline but soils remain warm. Under these conditions rapid recovery from undercutting and wrenching would result. A great length of new root, comparable to that which would be produced under warmer air and soil temperatures, would be

produced together with large numbers of short roots. In addition, height growth would be greatly reduced, but diameter growth enhanced, producing much sturdier as well as better balanced seedlings. As soils get colder, however, few roots would be produced and seedlings would be more susceptible to desiccation due to an inadequate root system. Thus such practices as undercutting and wrenching too late in the season could be hazardous and should be restricted to periods when favourable soil temperatures could be expected.

The final recovery experiment showed that root-pruning resulted in a drastic decline in the rate of photosynthesis and leaf water potential in the seedlings. Stomatal closure closely paralleled the decrease in photosynthesis. By day eight stomata were apparently tightly closed, and water potential was restored to the same level as prior to root-pruning but, at the expense of photosynthesis. After eight days under favourable environmental conditions, stomatal resistance declined, photosynthetic rates began to increase slowly and seedlings began producing roots. Seedlings had established contact with the soil and had an increased capacity to absorb more water and nutrients. By day thirty-two, the rates of photosynthesis had been restored to approximately 50-60% of the original value prior to root-pruning and seedlings were proliferating large numbers and lengths of new root and actively growing in both diameter and height. The results suggest that given favourable environmental conditions seedlings are capable of adjusting to the drastic alteration in their water relations due to root-pruning and of sustaining high rates of growth about three to four weeks after root-pruning.

All of the current studies took place in controlled environments, and it would be advisable to consider the applicability of the results in these terms. In the field and nursery, not only does temperature vary continuously but some or all of the other environmental factors such as moisture, nutrients and light also vary and are often limiting. The pattern of seedling growth will be influenced by all these factors in combination.

Within the limitations suggested above, several important characteristics of the species could be pointed out. Perhaps the most important is the remarkable ability of *P. radiata* for high RRP apparently all year round. Unlike most North European and North American conifers, which require a dormant or cold period to initiate a high rate of RRP, *P. radiata* showed no requirement for prior

exposure to reduced temperatures to regenerate roots. For *P. ponderosa* it has been shown that maximum root regeneration is largely controlled by the number of hours that seedlings in the nursery are exposed to low night temperatures (Schubert and Baron, 1965; Krugman and Stone, 1966; Stone, 1966, 1967a; Stone and Jenkinson, 1971). The *P. radiata* seedlings used in the current study were capable of proliferating large numbers of new roots when grown under a very wide range of environmental conditions with no preconditioning necessary. Seedlings were able to regenerate equally large numbers and lengths of new root when transferred from both high and low air temperatures, provided soil temperatures were optimal during the regeneration period.

P. radiata will function successfully over a wide range of air and soil temperatures and light conditions. Of the climatic factors examined only extremely high (40°C) soil temperature under an high air temperature (30°/20°C) severely restricted root growth and reduced survival.

Perhaps the most interesting result of the whole study is that seedlings lifted and planted in a cold climate are able to produce roots despite low air and soil temperatures. Although cold temperatures reduce the overall growth of newly planted seedlings some new roots are being produced. Once outplanted to the forest seedlings will thus quickly become adjusted to the new environment, achieve intimate contact with the soil and will be capable of absorbing essential moisture and nutrients. With increasing temperatures during the early spring months photosynthetic rates would be expected to rise, accompanied by a massive proliferation of the many root primordia formed during the cold months of winter immediately following outplanting. This response must account for much of the success of *P. radiata* when planted to the forest. Such a massive proliferation of new roots would render seedlings capable of taking full advantage of favourable environmental conditions early in the season.

Much of the technology of *P. radiata* establishment in recent years has concentrated on achieving very rapid early growth of seedlings once planted to the forest. Some of the results reported indicate quite spectacular success in achieving these objectives (for example, the reports for South Australia by Woods, 1976). It appears from the present studies that this quite spectacular success with *P. radiata* is due, at least in part, to the extraordinary capacity of

this species to proliferate a new root system under a wide range of environmental conditions. The species is not circumscribed in its physiological capacity for root growth by any need for preconditioning through cold temperatures or short day-length. The present studies have thus shown this to be yet another facet of the quite extraordinary capacity of *P. radiata* to grow and to develop into a most successful plantation tree under a very wide range of environmental conditions.

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APPENDIX I

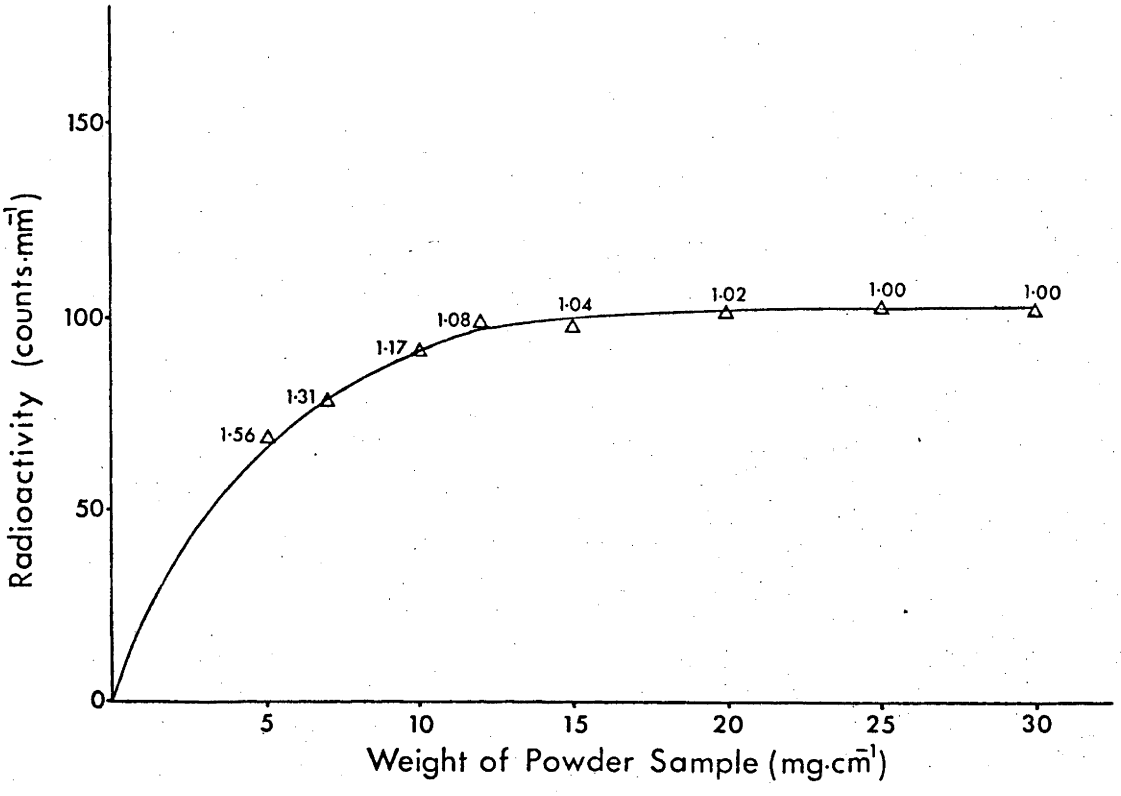
Composition of CERES Nutrient Solution

The nutrient solution is based on Hoagland (No.2) solution (E.J. Hewitt, Sand and Water Culture Methods used in the Study of Plant Nutrition, 2nd Edition 1966, pp.187-193) with some modification to minor elements.

Chemical Composition	Quantity (mg/l)	Elements (mg/l)
$Ca(NO_3)_2.4H_2O$	950	N 211.7
$(NH_4)H_2PO_4$	120	P 32.2
KNO_3	610	K 235.9
$MgSO_4.7H_2O$	490	Ca 160.9
H_3BO_3	0.60	Mg 48.3
$MnCl_2.4H_2O$	0.40	Na 3.61
$ZnSO_4.7H_2O$	0.09	S 66.7
$CuSO_4.5H_2O$	0.05	Cl 0.143
H_2MoO_4	0.02	Fe 5.007
$Co(NO_3)_2.6H_2O$	0.025	B 0.105
$FeSO_4.7H_2O$ (chelated with EDTA)	24.90	Co 0.005 Mn 0.111
NaOH	6.30	Cu 0.013
		Zn 0.02
		Mo 0.012

APPENDIX II

Infinite thickness curve for roots of *P. radiata* seedlings used to determine the correction factors for radioactivity of root powder samples less than the standard 30 mg. Each point represents one replicate. Values at each point are correction factors.



Correction factors for root powder samples less than 30 mg were determined as follows:

a) powder samples of 5, 7, 10, 12, 15, 20, 25 and 30 mg were drawn from a bulked sample of ground root material (4 seedlings).

b) radioactivity was counted for each sample as described in Chapter 3 and values plotted as counts per minute against the weight of the sample.

c) a curve was fitted using the 'freehand' method described by Nash (1965). From the values obtained from the curve, correction factors were calculated for each sample weight, using the following equation:

$$CF_x = ct_{30} \div ct_x$$

where CF_x = correction factor for powder sample less than 30 mg.

ct_{30} = radioactive count (counts.min^{-1}) for standard 30 mg powder sample.

ct_x = radioactive count (count.min^{-1}) for powder sample less than 30 mg.

d) for subsequent determination of radioactivity of samples less than the standard 30 mg, the radioactive counts for the samples were multiplied by the equivalent CF as determined from the curve.

APPENDIX III

Composition of nutrient solutions used in nutrient experiments (Chapter 4), expressed as the number of ml of stock solution per litre

Stock Solution	Prepared Nutrient Solutions (ml stock solution/litre)			
Chemical composition	FULL	-N	-P	-NP
1M $Ca(NO_3)_2.4H_2O$	5	-	5	-
1M $MgSO_4.7H_2O$	2	2	2	2
1M KH_2PO_4	1	1	-	-
1M KNO_3	5	-	5	-
1M $CaCl_2.6H_2O$	-	5	-	5
1M KCl	-	5	1	6
* Fe complex	1	1	1	1
** Micronutrients	1	1	1	1

* Fe complex - 0.031 M $FeCl_3$, 0.020M E.D.T.A. disodium salt $.2H_2O$

** Micronutrients = 0.046 M H_3BO_3, 0.009 M $MnCl_2.4H_2O$, 0.0008 M $ZnCl_2$, 0.0003 M $CuCl_2.2H_2O$, 0.0001 M Na_2MoO4.

Reference: Bachelard, E.P., Senior Lecturer, Forestry Department A.N.U.

APPENDIX IV.A. Summary of shoot growth, root growth and final dry weight of root-pruned and intact *P. radiata* seedlings under a day/night air temperature regime of 15°/5°C and soil temperatures of 5°C(1), 10°C(2), 15°C(3), 20°C(4) and 15°/5°C(5). Treatment means[1] and coefficients of variability (bracketed) are presented for each parameter.

A.1 SHOOT GROWTH

Experiment Number	Seedling Status	Initial Diameter (mm)		Initial Height (cm)		Diameter Increment (mm)		Height Increment (cm)		RGR Increment (mm/mm/day)		RGR Height (cm/cm/day)	
4	Root-Pruned	4.06(6.4)	2	18.49(7.2)	2	0.75(34.4)	5	0.59(>100.0)	5	0.0079(26.6)	5	0.0015(1.0)	5
		4.10(6.0)	3	18.70(17.4)	5	0.76(19.2)	2	0.69(60.0)	2	0.0081(14.8)	2	0.0017(58.8)	2
		4.10(5.8)	5	18.78(8.6)	3	0.86(33.4)	3	0.70(55.6)	3	0.0094(18.1)	3	0.0017(60.0)	3
	Intact	4.74(1.9)	5	20.75(8.5)	2	1.39(8.1)	2	1.80(31.4)	2	0.0120(5.8)	2	0.0037(2.7)	5
		4.80(0.7)	3	20.85(28.2)	3	1.41(12.0)	3	1.80(62.8)	3	0.0125(14.4)	3	0.0040(40.0)	2
		4.82(1.0)	2	24.15(20.8)	5	1.68(1.7)	5	1.95(25.4)	5	0.0144(3.5)	5	0.0044(79.5)	3
5	Root-Pruned	6.08(6.5)	1	26.55(10.9)	4	0.78(39.8)	1	0.80(71.6)	1	0.0057(35.1)	1	0.0014(71.4)	1
		6.15(6.2)	4	27.15(5.6)	1	0.96(24.2)	4	0.94(47.7)	4	0.0068(22.1)	4	0.0017(41.2)	4
	Intact	4.84(2.5)	4	16.65(5.5)	4	0.84(58.4)	4	0.60(23.5)	4	0.0075(53.3)	4	0.0017(0.0)	4
		4.92(0.3)	1	19.10(19.5)	1	1.26(11.8)	1	0.90(62.9)	1	0.0108(9.3)	1	0.0021(47.6)	1

A.2 ROOT GROWTH

Experiment Number	Seedling Status	Number of New Roots 0.1-1.4cm(SR)	Number of New Roots ≥1.5cm(LR)	Total Number of New Roots ≥0.1cm(GT)	Total Length of New Roots ≥0.1cm(TL)*	Average Length of New Roots ≥0.1cm(AL)*	Number of White Root Tips	Diameter of White Root Tips (mm)
4	Root-Pruned	75(44.0) 2	5(79.2) 2	80(42.5) 2	48.1(54.3) 2	0.58(25.0) 2		
		180(55.2) 5	58(89.6) 5	238(53.2) 5	248.8(70.7) 5	0.99(23.0) 5		
		184(60.0) 3	77(63.5) 3	261(59.6) 3	303.6(64.2) 3	1.08(28.1) 3		
	Intact						446(37.0) 3	2.24(21.2) 3
							561(20.9) 5	2.28(7.1) 5
							566(1.1) 2	2.44(8.1) 2
5	Root-Pruned	51(74.5) 1	4(>100.0) 1	55(67.4) 1	40.4(77.7) 1	0.73(46.9) 1		
		70(48.6) 4	79(54.4) 4	149(46.3) 4	323.8(64.9) 4	2.08(34.9) 4		
	Intact						92(16.3) 4	1.54(2.7) 1
							386(59.3) 1	2.12(6.0) 4

* Root lengths in cm.

A.3 FINAL DRY WEIGHT

Experiment Number	Seedling Status	Shoot Dry Weight(g)	New Root Dry Weight(g)	Total Root Dry Weight(g)	Root:Shoot Ratio
4	Root-Pruned	5.105(15.5) 3	0.034(51.5) 2	1.881(17.2) 5	0.36(11.9) 5
		5.282(25.3) 2	0.112(59.5) 5	2.004(11.9) 2	0.39(10.2) 2
		5.530(30.3) 5	0.138(49.8) 3	2.067(14.0) 3	0.41(10.2) 3
	Intact	6.431(1.4) 3	0.500(39.1) 3	4.150(13.4) 2	0.49(16.4) 2
		8.583(12.5) 2	0.622(12.4) 2	4.775(4.2) 3	0.60(2.3) 5
		8.788(11.6) 5	0.944(25.4) 5	5.244(3.0) 5	0.74(6.0) 3
5	Root-Pruned	12.981(21.1) 4	0.020(73.0) 1	3.690(12.2) 1	0.27(10.1) 1
		13.602(13.8) 1	0.264(62.4) 4	4.432(15.0) 4	0.34(8.7) 4
	Intact	5.487(13.2) 4	0.172(26.7) 4	4.223(10.0) 1	0.50(4.6) 1
		8.231(1.4) 1	0.380(46.4) 1	4.120(8.6) 4	0.78(10.0) 4

1 Mean of 8 and 2 replicates for root-pruned and intact seedlings respectively.

Note: Vertical lines join treatment means that are not significantly different at $P_{0.05}$ according to Duncan's multiple range test (Experiment 4) and Student's t-test (Experiment 5).

APPENDIX IV.B. Summary of shoot growth, root growth and final dry weight of root-pruned and intact *P. radiata* seedlings under a day/night air temperature regime of 20°/10°C and soil temperatures of 10°C(1), 15°C(2), 20°C(3), 25°C(4) and 20°/10°C(5). Treatment means[1] and coefficients of variability (bracketed) are presented for each parameter.

B.1 SHOOT GROWTH

Experiment Number	Seedling Status	Initial Diameter (mm)		Initial Height (cm)		Diameter Increment (mm)		Height Increment (cm)		RGR Increment (mm/mm/day)		RGR Height (cm/cm/day)	
6	Root-Pruned	4.04(5.7)	2	17.05(8.0)	1	0.44(32.9)	1	1.54(39.1)	2	0.0048(29.2)	1	0.0041(39.0)	2
		4.04(5.9)	1	17.44(7.3)	2	0.62(40.2)	2	1.60(25.0)	5	0.0069(38.2)	2	0.0041(31.7)	5
		4.29(9.4)	5	18.01(5.9)	5	0.75(44.3)	5	1.84(50.1)	1	0.0075(40.0)	5	0.0047(42.6)	1
	Intact	3.75(19.8)	2	15.25(14.4)	5	1.33(11.6)	2	2.85(22.3)	5	0.0146(18.5)	2	0.0080(47.5)	1
		3.92(13.2)	1	16.07(28.0)	2	1.49(7.4)	1	2.93(3.9)	2	0.0156(10.9)	1	0.0083(20.5)	2
		4.16(15.5)	5	17.87(17.9)	1	1.68(7.1)	5	3.33(58.6)	1	0.0163(6.8)	5	0.0083(33.7)	5
7	Root-Pruned	3.72(6.6)	3	8.26(6.9)	4	1.29(18.7)	4	2.16(40.7)	3	0.0136(22.1)	3	0.0115(17.4)	4
		3.73(5.8)	4	8.49(9.4)	3	1.36(9.9)	3	2.25(19.0)	4	0.0141(14.2)	4	0.0141(70.9)	3
	Intact	4.29(4.8)	3	11.13(9.0)	3	1.56(14.0)	3	3.97(21.0)	4	0.0148(13.5)	3	0.0144(13.9)	4
		4.36(1.6)	4	11.77(4.2)	4	1.96(12.9)	4	4.80(29.4)	3	0.0176(11.4)	4	0.0169(23.7)	3
8	Root-Pruned	5.13(4.6)	3	20.09(2.5)	3	0.23(53.7)	3	1.00(51.6)	4	0.0021(54.0)	3	0.0023(46.3)	4
		5.19(4.7)	4	20.43(5.9)	4	0.29(58.2)	4	1.27(36.3)	3	0.0426(49.7)	4	0.0025(31.4)	3
	Intact	5.53(8.2)	3	22.75(1.6)	4	0.58(27.9)	4	1.90(7.4)	4	0.0047(25.3)	4	0.0036(8.0)	4
		5.68(3.3)	4	23.40(0.6)	3	1.00(29.2)	3	2.45(14.4)	3	0.0078(32.1)	3	0.0043(16.2)	3

B.2 ROOT GROWTH

Experiment Number	Seedling Status	Number of New Roots 0.1-1.4cm(SR)	Number of New Roots ≥1.5cm(LR)	Total Number of New Roots ≥0.1cm(GT)	Total Length of New Roots ≥0.1cm(TL)*	Average Length of New Roots ≥0.1cm(AL)*	Number of White Root Tips	Diameter of White Root Tips (mm)
6	Root-Pruned	4(>100.0) 1	0(0.0) 1	4(>100.0) 1	2.3(96.4) 1	0.64(60.0) 1		
		32(>100.0) 2	15(>100.0) 2	47(>100.0) 2	60.6(>100.0) 2	1.01(57.6) 2		
		44(67.8) 5	24(>100.0) 5	68(73.3) 5	99.4(>100.0) 5	1.17(57.6) 5		
	Intact						179(12.8) 1	1.77(40.2) 2
							214(26.7) 5	2.10(21.2) 5
							221(37.4) 2	2.16(32.7) 1
7	Root-Pruned	41(78.03) 3	82(>100.0) 3	123(77.2) 3	394.3(90.1) 3	3.05(18.4) 4		
		64(34.4) 4	108(43.5) 4	172(36.0) 4	516.8(36.0) 4	3.07(19.2) 3		
	Intact						235(9.6) 4	1.52(13.4) 4
							276(41.5) 3	1.82(15.2) 3
8	Root-Pruned	6(>100.0) 3	2(>100.0) 3	6(95.4) 3	3.5(70.5) 3	0.58(88.6) 3		
		48(62.1) 4	5(100.0) 4	53(62.5) 4	43.6(83.8) 4	0.79(53.8) 4		
	Intact						30(89.6) 4	1.48(11.5) 4
							218(22.7) 3	1.68(18.2) 3

* Root lengths in cm.

B.3 FINAL DRY WEIGHT

Experiment Number	Seedling Status	Shoot Dry Weight(g)		New Root Dry Weight(g)		Total Root Dry Weight(g)		Root:Shoot Ratio	
6	Root-Pruned	4.694(20.5)	1	0.001(>100.0)	1	0.992(14.4)	1	0.22(12.3)	1
		4.928(13.7)	2	0.022(>100.0)	2	1.303(19.1)	5	0.23(4.1)	5
		5.704(20.1)	5	0.063(>100.0)	5	1.312(40.8)	2	0.26(16.4)	2
	Intact	5.587(19.8)	2	0.510(43.2)	2	2.484(33.0)	1	0.42(19.6)	1
		6.066(38.5)	1	0.589(82.3)	1	2.647(23.0)	2	0.49(38.0)	5
		6.638(00.0)	5	0.595(55.4)	5	3.236(59.0)	5	0.49(21.8)	2
7	Root-Pruned	4.292(15.4)	4	0.308(26.6)	4	1.897(18.4)	3	0.43(9.4)	3
		4.425(18.6)	3	0.350(18.6)	3	2.032(15.0)	4	0.48(11.4)	4
	Intact	6.368(9.9)	3	0.279(5.7)	4	3.337(11.9)	3	0.48(7.0)	4
		7.600(13.7)	4	0.473(38.2)	3	3.583(6.2)	4	0.53(11.2)	3
8	Root-Pruned	6.910(13.4)	3	0.002(95.2)	3	1.845(14.3)	4	0.24(17.0)	4
		7.749(13.9)	4	0.021(>100.0)	4	1.888(15.8)	3	0.28(20.2)	3
	Intact	9.480(2.6)	4	0.062(75.8)	4	3.575(7.8)	4	0.36(7.8)	3
		11.050(8.4)	1	0.379(30.3)	3	4.002(16.3)	3	0.38(5.6)	4

1 Mean of 8 and 2 replicates for root-pruned and intact seedlings respectively.

Note: Verticle lines join treatment means that are not significantly different at $P_{0.05}$ according to Duncan's multiple range test (Experiment 6) and Student's t-test (Experiment 7 and 8).

APPENDIX IV.C. Summary of shoot growth, root growth and final dry weight of root-pruned and intact *P. radiata* seedlings under a day/night air temperature regime of 25°/15°C and soil temperatures of 10°C(1), 15°C(2), 20°C(3), 25°C(4), 30°C(5), 35°C(6) and 25°/15°C(7). Treatment means[1] and coefficients of variability (bracketed) are presented for each parameter.

C.1 SHOOT GROWTH

Experiment Number	Seedling Status	Initial Diameter (mm)		Initial Height (cm)		Diameter Increment (mm)		Height Increment (cm)		RGR Increment (mm/mm/day)		RGR Height (cm/cm/day)	
9	Root-Pruned	4.33(5.2)	1	21.34(9.8)	4	0.29(59.1)	2	1.71(38.7)	7	0.0030(56.7)	2	0.0036(33.3)	7
		4.34(4.9)	7	21.40(7.8)	2	0.30(42.8)	7	1.92(19.3)	2	0.0031(41.9)	1	0.0040(12.5)	1
		4.35(4.1)	2	21.56(10.2)	7	0.32(39.3)	1	1.92(17.0)	4	0.0032(37.5)	7	0.0041(22.0)	2
		4.35(4.5)	3	21.61(9.5)	3	0.38(50.6)	3	1.94(17.0)	1	0.0040(50.0)	3	0.0041(19.5)	4
		4.40(5.5)	4	21.94(6.7)	1	0.41(35.5)	4	2.04(27.4)	3	0.0042(33.3)	4	0.0043(30.2)	3
	Intact	4.17(28.1)	4	20.80(28.6)	3	1.26(60.1)	4	2.20(51.4)	3	0.0120(31.7)	4	0.0046(23.9)	3
		4.24(25.9)	2	20.85(24.8)	1	1.27(26.7)	1	2.70(63.0)	4	0.0121(4.1)	1	0.0052(44.2)	4
		4.36(22.2)	1	21.25(21.6)	2	1.40(47.1)	2	3.15(29.2)	2	0.0132(19.7)	2	0.0065(7.7)	2
		4.40(30.0)	3	22.15(20.1)	4	1.44(18.2)	7	3.25(15.4)	1	0.0133(19.5)	3	0.0069(8.7)	1
		4.42(12.8)	7	22.25(20.7)	7	1.48(50.7)	3	4.35(11.5)	7	0.0135(26.7)	7	0.0086(7.0)	7
10	Root-Pruned	4.36(8.6)	4	17.55(5.9)	3	0.28(59.5)	4	0.74(61.0)	6	0.0031(54.8)	4	0.0019(57.9)	6
		4.39(8.2)	5	17.60(8.0)	5	0.36(47.8)	3	0.98(43.8)	4	0.0036(44.4)	3	0.0025(36.0)	4
		4.41(7.8)	6	17.60(8.4)	6	0.38(52.7)	6	1.04(51.5)	3	0.0040(55.0)	6	0.0027(48.1)	3
		4.45(8.6)	3	17.81(7.2)	4	0.44(44.6)	5	1.12(31.4)	5	0.0045(42.2)	5	0.0030(30.0)	5
	Intact	4.39(2.9)	5	21.75(1.6)	5	0.86(21.0)	5	1.70(16.6)	5	0.0079(13.9)	4	0.0037(24.3)	5
		4.54(1.4)	6	21.80(1.3)	4	0.88(20.6)	4	1.95(40.0)	4	0.0085(21.8)	5	0.0043(25.6)	4
		4.71(2.1)	3	22.10(0.6)	6	1.07(59.8)	3	2.50(>100.0)	3	0.0095(52.6)	3	0.0047(>100.0)	3
		4.82(4.5)	4	22.50(1.3)	3	1.94(1.1)	6	3.40(58.2)	2	0.0169(2.4)	6	0.0067(55.2)	6
11	Root-Pruned	5.03(9.2)	2	20.89(11.0)	7	0.05(90.9)	1	0.26(94.9)	1	0.0025(34.0)	1	0.0006(31.0)	1
		5.05(9.1)	7	21.69(9.5)	1	0.20(55.2)	7	0.60(80.0)	7	0.0019(27.4)	7	0.0014(42.3)	2
		5.22(11.1)	1	22.51(7.0)	2	0.25(>100.0)	2	0.73(51.2)	2	0.0022(49.1)	2	0.0016(54.4)	7
	Intact	4.62(9.0)	1	16.30(0.0)	7	0.74(7.6)	1	1.00(0.0)	2	0.0074(7.1)	1	0.0045(31.0)	2
		4.75(0.0)	7	17.50(0.0)	2	0.86(0.0)	2	1.20(0.0)	7	0.0093(18.0)	2	0.0029(43.5)	1
		5.03(0.0)	2	19.85(6.1)	1	0.88(0.0)	7	1.25(5.7)	1	0.0085(5.8)	7	0.0050(30.2)	7

C.2 ROOT GROWTH

Experiment Number	Seedling Status	Number of New Roots 0.1-1.4cm(SR)	Number of New Roots ≥1.5cm(LR)	Total Number of New Roots ≥0.1cm(GT)	Total Length of New Roots ≥0.1cm(TL)*	Average Length of New Roots ≥0.1cm(AL)*	Number of White Root Tips	Diameter of White Root Tips (mm)
9	Root-Pruned	35(80.0) 1 105(69.5) 2 122(29.5) 4 124(64.5) 7 142(59.2) 3	1(>100.0)1 5(>100.0)2 66(>100.0)3 84(67.2) 4 87(>100.0)7	36(77.8) 1 110(72.5) 2 206(28.2) 4 208(67.7) 3 211(87.4) 7	16.2(78.5) 1 58.5(82.6) 2 243.3(97.5) 3 382.8(>100.0) 7 420.1(47.4) 4	0.52(28.0) 1 0.52(23.3) 2 1.10(42.0) 3 1.55(48.3) 7 2.02(42.1) 4		
	Intact						403(73.9) 4 443(56.9) 1 449(24.3) 2 610(75.9) 3 586(22.0) 7	1.38(2.6) 4 1.66(10.8) 7 1.84(2.3) 3 2.04(10.0) 2 2.17(1.3) 1
10	Root-Pruned	11(>100.0) 6 91(70.6) 4 135(63.0) 5 178(61.2) 3	0(0.0) 6 26(>100.0)5 27(77.8) 3 64(64.1) 4	11(>100.0) 6 155(63.2) 4 161(65.8) 5 205(62.4) 3	3.2(>100.0) 6 154.7(92.1) 5 171.2(61.1) 3 264.9(63.4) 7	0.28(51.9) 6 0.86(12.6) 3 0.96(48.0) 5 1.73(38.5) 4		
	Intact						58(94.7) 6 168(>100.0)4 292(36.8) 5 310(67.7) 3	1.12(33.0) 4 1.41(19.1) 6 1.52(5.2) 3 1.75(2.4) 5
11	Root-Pruned	38(46.8) 1 56(43.0) 2 108(41.9) 7	6(>100.0) 1 31(65.4) 2 35(51.4) 7	44(53.5) 1 87(44.8) 2 136(37.5) 7	35.0(80.6) 1 121.8(48.1) 2 148.8(41.0) 7	0.72(32.2) 1 1.06(18.2) 7 1.38(39.6) 2		
	Intact						80(0.0) 2 132(12.9) 1 200(0.0) 7	1.36(0.0) 7 1.68(0.0) 2 1.76(15.3) 1

* Root lengths in cm.

C.3 FINAL DRY WEIGHT

Experiment Number	Seedling Status	Shoot Dry Weight (g)		New Root Dry Weight(g)		Total Root Dry Weight(g)		Root:Shoot Ratio	
9	Root-Pruned	4.967(10.8)	2	0.017(>100.0)	1	1.268(12.6)	1	0.25(6.4)	1
		5.088(16.4)	1	0.018(89.1)	2	1.270(13.9)	2	0.25(7.3)	3
		5.480(11.2)	7	0.085(79.8)	3	1.436(16.3)	3	0.26(8.6)	2
		5.720(20.8)	3	0.144(46.4)	4	1.546(19.0)	7	0.28(5.9)	4
		5.755(11.5)	4	0.162(90.5)	7	1.594(19.0)	4	0.28(5.6)	7
	Intact	6.658(62.6)	4	0.330(70.3)	4	2.754(34.0)	1	0.40(20.3)	1
		7.331(53.5)	2	0.430(31.3)	1	4.138(54.4)	2	0.56(0.8)	2
		7.684(63.9)	1	0.459(44.2)	3	4.258(62.7)	4	0.58(2.6)	7
		7.912(74.2)	3	0.692(8.8)	7	4.576(66.9)	3	0.60(6.7)	3
		9.479(24.2)	7	0.700(54.6)	2	5.478(20.5)	7	0.64(0.1)	4
10	Root-Pruned	4.835(24.1)	6	0.008(>100.0)	6	1.410(18.0)	4	0.30(10.8)	4
		4.844(21.9)	4	0.048(37.8)	3	1.456(23.1)	6	0.30(13.1)	5
		4.921(22.7)	3	0.049(49.7)	5	1.475(16.8)	3	0.31(9.8)	3
		5.170(22.5)	5	0.081(51.9)	4	1.516(15.6)	5	0.31(16.7)	6
	Intact	7.701(19.6)	5	0.049(87.6)	6	3.106(9.2)	6	0.35(0.5)	6
		8.081(15.5)	4	0.156(>100.0)	4	3.594(19.8)	5	0.43(9.6)	3
		8.874(9.9)	6	0.356(60.4)	5	3.934(59.6)	4	0.43(0.1)	5
		9.152(33.1)	3	0.535(78.6)	3	4.043(47.6)	3	0.47(29.4)	4
11	Root-Pruned	7.078(29.3)	7	0.009(90.3)	1	1.950(12.1)	1	0.28(11.1)	1
		7.235(22.7)	1	0.037(46.2)	7	2.028(20.1)	7	0.29(12.4)	7
		7.286(24.1)	2	0.054(61.0)	2	2.187(16.8)	2	0.30(11.5)	2
	Intact	6.154(0.0)	7	0.135(0.0)	7	3.616(0.0)	7	0.53(18.7)	1
		7.492(29.8)	1	0.153(0.0)	2	3.883(12.2)	1	0.58(0.0)	2
		8.174(0.0)	2	0.191(14.1)	1	4.755(0.0)	2	0.59(0.0)	7

1 Mean of 8 and 2 replicates for root-pruned and intact seedlings respectively.

Note: Vertical lines join treatment means that are not significantly different at $P_{0.05}$ according to Duncan's multiple range test.

APPENDIX IV.D. Summary of shoot growth, root growth and final dry weight of root-pruned and intact *P. radiata* seedlings under a day/night air temperature regime of 30°/20°C and soil temperatures of 15°C(1), 20°C(2), 25°C(3), 30°C(4), 35°C(5), 40°C(6) and 30°/20°C(7). Treatment means[1] and coefficients of variability (bracketed) are presented for each parameter.

D.1 SHOOT GROWTH

Experiment Number	Seedling Status	Initial Diameter (mm)	Initial Height (cm)	Diameter Increment (mm)	Height Increment (cm)	RGR Increment (mm/mm/day)	RGR Height (cm/cm/day)
12	Root-Pruned	3.77(9.4) 7	13.35(12.3) 1	0.25(37.8) 2	1.10(54.3) 3	0.0030(40.0) 2	0.0034(52.9) 3
		3.78(10.4) 4	14.06(21.4) 4	0.26(58.6) 1	1.42(64.3) 1	0.0031(51.6) 1	0.0048(60.4) 1
		3.80(10.8) 3	14.24(14.2) 3	0.39(44.7) 3	1.71(27.8) 7	0.0047(36.2) 7	0.0054(29.6) 7
		3.81(11.1) 1	14.61(17.4) 7	0.39(35.5) 7	1.88(28.2) 4	0.0048(52.1) 3	0.0060(23.3) 4
		3.82(11.3) 2	14.66(14.2) 2	0.48(37.8) 4	2.20(22.9) 2	0.0059(40.7) 4	0.0067(20.9) 2
	Intact	3.10(3.4) 1	10.25(0.7) 2	0.53(26.7) 2	1.40(0.0) 2	0.0075(32.0) 2	0.0061(0.0) 2
		3.12(1.1) 3	10.50(6.7) 7	0.60(37.7) 1	1.95(3.6) 3	0.0083(30.1) 1	0.0079(10.1) 3
		3.12(2.0) 4	10.75(16.4) 4	0.84(2.5) 3	2.40(23.6) 1	0.0114(0.9) 3	0.0094(11.7) 1
		9.12(8.0) 2	10.85(15.0) 3	0.98(31.2) 7	2.95(21.6) 4	0.0124(17.7) 7	0.0115(5.2) 4
		3.22(12.1) 7	10.90(11.7) 1	1.18(14.9) 4	3.35(2.1) 7	0.0153(14.4) 4	0.0132(7.6) 7
13	Root-Pruned	4.29(5.0) 4	18.24(9.4) 5	0.17(>100.0) 6	0.56(93.1) 6	0.0017(>100.0) 6	0.0014(92.9) 6
		4.29(5.7) 5	18.40(8.0) 6	0.29(62.2) 3	1.01(52.6) 3	0.0031(58.1) 3	0.0025(52.0) 3
		4.30(6.5) 6	18.42(10.0) 3	0.38(55.6) 4	1.72(49.8) 4	0.0040(52.5) 4	0.0041(46.3) 4
		4.30(5.8) 3	18.86(10.0) 4	0.60(35.9) 5	1.82(27.4) 5	0.0061(32.8) 5	0.0046(26.1) 5
	Intact	3.53(7.6) 4	13.75(2.6) 4	0.42(>100.0) 3	1.40(>100.0) 3	0.0046(>100.0) 3	0.0042(>100.0) 3
		3.66(2.9) 5	14.55(0.5) 3	0.89(42.9) 4	2.35(15.0) 4	0.0105(32.4) 4	0.0065(12.3) 6
		3.68(0.2) 6	15.15(1.4) 5	1.37(3.1) 5	2.40(5.9) 6	0.0151(5.3) 5	0.0074(44.6) 5
		3.72(9.5) 3	16.25(6.5) 6	1.58(5.4) 6	2.60(4.9) 5	0.0170(4.1) 6	0.0075(16.0) 4

D.2 ROOT GROWTH

Experiment Number	Seedling Status	Number of New Roots 0.1-1.4cm(SR)	Number of New Roots ≥1.5cm(LR)	Total Number New Roots ≥0.1cm(GT)	Total Length of New Roots ≥0.1cm(TL)*	Average Length of New Roots ≥0.1cm(AL)*	Number of White Root Tips	Diameter of White Root Tips (mm)
12	Root-Pruned	77(77.2) 3 93(55.6) 7 103(53.8) 4 121(59.5) 1 124(69.1) 2	38(90.4) 1 94(89.4) 3 104(60.7) 7 110(58.7) 2 114(63.2) 4	159(76.2) 1 171(83.0) 3 197(49.3) 7 217(57.4) 4 234(50.5) 2	164.4(78.6) 1 395.2(88.9) 3 433.2(55.3) 2 452.7(61.5) 7 597.2(71.0) 4	1.01(46.4) 1 1.79(34.6) 2 2.22(33.7) 7 2.27(23.6) 3 2.51(52.8) 4		
	Intact						98(37.0) 2 196(60.1) 7 215(39.5) 3 283(27.0) 1 337(32.3) 4	1.20(2.9) 2 1.24(10.9) 4 1.24(14.5) 3 1.42(22.9) 7 1.52(14.5) 1
13	Root-Pruned	0(0.0) 6 26(>100.0) 5 94(61.7) 3 132(65.7) 4	0(0.0) 6 3(>100.0) 5 36(>100.0) 4 37(>100.0) 3	0(0.0) 6 29(>100.0) 5 130(71.5) 3 169(69.2) 4	0.0(0.0) 6 18.8(>100.0) 5 150.9(>100.0) 4 181.3(90.8) 3	0.0(0.0) 6 0.41(70.6) 5 0.70(62.3) 4 1.25(32.0) 3		
	Intact						0(0.0) 6 14(>100.0) 3 51(11.8) 5 202(95.1) 4	0.00(0.0) 6 0.50(>100.0) 3 1.19(0.0) 5 1.65(36.8) 4

* Root lengths in cm.

D.3 FINAL DRY WEIGHT

Experiment Number	Seedling Status	Shoot Dry Weight(g)		New Root Dry Weight(g)		Total Root Dry Weight(g)		Root:Shoot Ratio	
12	Root-Pruned	3.93(12.9)	3	0.054(61.3)	1	1.13(20.7)	2	0.28(11.0)	2
		4.10(27.0)	2	0.122(51.5)	2	1.21(19.8)	1	0.29(9.3)	1
		4.19(22.0)	1	0.132(65.5)	3	1.28(26.4)	5	0.30(7.6)	4
		4.27(25.7)	7	0.160(66.7)	7	1.37(16.1)	3	0.30(9.9)	5
		4.70(30.2)	4	0.202(70.4)	4	1.41(32.6)	4	0.35(8.0)	3
	Intact	2.720(7.2)	2	0.135(21.2)	3	1.670(28.8)	4	0.44(1.8)	4
		3.034(20.6)	1	0.190(42.5)	4	1.736(0.7)	2	0.62(8.0)	7
		3.186(7.5)	3	0.229(3.5)	2	1.920(28.9)	1	0.62(1.5)	3
		3.752(33.2)	7	0.234(45.3)	7	1.988(7.8)	3	0.63(6.0)	1
		3.828(1.6)	4	0.515(43.0)	1	2.196(21.8)	7	0.64(4.6)	2
13	Root-Pruned	4.38(18.9)	6	0.000(0.0)	6	1.08(20.9)	6	0.25(6.5)	6
		4.65(18.8)	3	0.007(0.0)	5	1.31(19.2)	4	0.26(7.1)	5
		5.05(17.1)	4	0.053(>100.0)	4	1.33(26.7)	5	0.26(13.0)	4
		5.15(20.9)	5	0.064(74.0)	3	1.36(16.4)	3	0.30(9.6)	3
	Intact	3.800(52.5)	3	0.000(0.0)	6	1.454(52.5)	3	0.29(0.4)	6
		4.338(36.6)	4	0.014(>100.0)	3	1.692(16.6)	6	0.35(0.0)	5
		5.232(2.6)	5	0.038(35.7)	5	1.826(2.8)	5	0.38(0.1)	3
		5.844(15.7)	6	0.191(99.7)	4	1.938(57.1)	4	0.43(14.0)	4

1 Mean of 8 and 2 replicates for root-pruned and intact seedlings respectively.

Note: Vertical lines join treatment means that are not significantly different at $P_{0.05}$ according to Duncan's multiple range test.

APPENDIX V

Effect of various combinations of air and soil temperature on net photosynthesis of root-pruned and intact seedlings. Bracketed values indicate soil temperatures in °C. 'A' represents soil temperatures the same as air temperatures.

Experiment Number	Day/Night Air Temperature (°C)	Net Photosynthesis ($mg.g^{-1}.hr^{-1}$)[1]	
		Root-Pruned Seedlings	Intact Seedlings
4	15/5	4.62 (10) 6.83 (A) 6.84 (15)	7.77 (10) 10.78 (A) 12.82 (15)
5	15/5	3.16 (5) 5.32 (A) 6.85 (20)	4.58 (5) 9.32 (20) 10.68 (A)
6	20/10	5.48 (15) 6.11 (A) 7.32 (10)	7.11 (15) 9.22 (10) 9.45 (A)
7	20/10	9.54 (20) 11.08 (25)	11.16 (20) 13.80 (25)
8	20/10	4.30 (A) 5.83 (25) 5.90 (20)	5.92 (A) 6.27 (25) 7.04 (20)
9	25/15	3.09 (10) 3.46 (15) 3.46 (20) 3.67 (A) 3.86 (25)	7.57 (10) 9.72 (15) 10,03 (20) 10.27 (A) 10.92 (25)
10	25/15	5.00 (30) 5.29 (35) 6.51 (25) 6.89 (20)	5.89 (30) 6.19 (25) 7.29 (35) 9.48 (20)
11	25/15	3.32 (20) 6.53 (25) 7.92 (A)	9.11 (20) 9.24 (25) 11.32 (A)
12	30/20	6.31 (30) 7.19 (25) 7.30 (A) 7.53 (20) 9.72 (15)	7.13 (20) 8.71 (15) 9.04 (30) 9.56 (A) 9.70 (25)
13	30/20	4.47 (25) 4.49 (40) 7.59 (35) 7.70 (30)	5.82 (40) 7.44 (35) 7.74 (25) 9.25 (30)

1 Mean of 2 replicates for root-pruned and intact seedlings.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ according to Duncan's multiple range test (Experiments 3, 5, 8-12) and Student's t-test (Experiments 4, 6, 7).

APPENDIX VI

Effects of various soil and air temperatures on the distribution of ^{14}C-photosynthate in both root-pruned and intact seedlings three weeks after ^{14}C-labelling. Bracketed values indicate soil temperatures in ^{o}C. 'A' represents soil temperature the same as air temperature .

Experiment Number	Day/Night Air Temperature (^{o}C)	Seedling Part	^{14}C Activity (% of total plant recovery)	
			Root-Pruned Seedlings[1]	Intact Seedlings[2]
4	15/5	Total Shoot	74.6 (15) 78.0 (10) 78.8 (A)	61.0 (15) 66.1 (A) 70.2 (10)
		stem	57.5 (15) 63.4 (10) 66.4 (A)	38.1 (10) 45.9 (15) 48.2 (A)
		branches	12.4 (A) 14.6 (10) 17.1 (15)	14.5 (A) 18.1 (15) 31.9 (10)
		Total Root	20.7 (A) 22.3 (10) 25.4 (15)	29.9 (10) 34.0 (A) 39.0 (15)
		residual root	20.2 (A) 21.8 (10) 24.2 (15)	24.2 (10) 32.2 (A) 36.9 (15)
		new root	0.2 (10) 0.5 (A) 1.2 (15)	1.8 (A) 2.1 (15) 5.7 (10)
5	15/5	Total Shoot	78.7 (20) 86.7 (5)	58.2 (20) 67.2 (5)
		stem	59.4 (20) 59.9 (5)	41.6 (20) 55.1 (5)
		branches	19.3 (20) 30.0 (5)	11.9 (5) 16.6 (20)
		Total Root	10.1 (5) 21.3 (20)	32.6 (5) 41.6 (20)
		residual root	10.2 (5) 20.8 (20)	27.1 (5) 41.1 (20)
		new root	0.0* (5) 0.5 (20)	0.5 (20) 5.6 (5)
6	20/10	Total Shoot	82.1 (15) 87.8 (A) 92.3 (10)	73.0 (A) 75.1 (15) 80.1 (10)
		stem	56.0 (15) 61.0 (10) 62.6 (A)	42.0 (A) 43.8 (15) 59.7 (10)
		branches	24.9 (A) 26.1 (15) 31.2 (10)	20.4 (10) 31.0 (A) 31.3 (15)
		Total Root	7.7 (10) 12.2 (A) 18.0 (15)	20.0 (10) 24.7 (15) 27.0 (A)
		residual root	7.7 (10) 12.2 (A) 17.9 (15)	18.6 (10) 22.4 (15) 25.2 (A)
		new root	0.0* (10) 0.1 (15) 0.1 (A)	1.4 (10) 1.8 (A) 2.3 (15)
7	20/10	Total Shoot	78.1 (25) 83.1 (20)	65.8 (20) 79.8 (25)
		stem	46.7 (20) 48.2 (25)	27.1 (20) 37.0 (25)
		branches	29.7 (25) 36.3 (20)	33.8 (25) 38.7 (20)
		Total Root	16.9 (20) 21.9 (25)	29.2 (25) 34.2 (20)
		residual root	15.3 (20) 21.1 (25)	28.6 (25) 32.7 (20)
		new root	0.8 (25) 1.5 (20)	0.6 (25) 1.5 (20)

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APPENDIX VI (Cont'd)

Experiment Number	Day/Night Air Temperature (°C)	Seedling Part	^{14}C Activity (% of total plant recovery)									
			Root-Pruned Seedlings[1]					Intact Seedlings[2]				
9	25/15	Total Shoot	87.4 (20)	88.6 (25)	89.9 (A)	92.0 (15)	94.0 (10)	71.8 (25)	73.8 (20)	75.5 (A)	78.2 (15)	80.0 (10)
		stem	63.3 (A)	63.4 (25)	66.8 (20)	72.5 (15)	77.1 (10)	45.7 (20)	46.8 (A)	50.1 (15)	52.6 (25)	64.8 (10)
		branches	16.9 (10)	19.1 (15)	20.6 (20)	25.2 (25)	26.6 (A)	15.2 (10)	19.2 (25)	28.1 (15)	28.1 (20)	28.7 (A)
		Total Root	6.0 (10)	8.1 (15)	10.1 (A)	11.7 (25)	12.5 (20)	20.7 (10)	21.8 (15)	24.4 (A)	26.1 (20)	28.2 (25)
		residual root	6.0 (10)	7.9 (15)	10.0 (A)	11.2 (25)	12.1 (20)	14.9 (10)	20.4 (15)	23.4 (A)	25.5 (20)	27.8 (25)
		new root	0.0* (10)	0.1 (A)	0.2 (15)	0.4 (20)	0.5 (25)	0.4 (25)	0.6 (20)	1.0 (A)	1.4 (15)	5.8 (10)
10	25/15	Total Shoot	85.1 (30)	85.3 (35)	89.4 (20)	91.2 (25)		72.3 (35)	73.1 (30)	74.1 (25)	84.0 (20)	
		stem	53.8 (35)	57.6 (30)	58.8 (20)	64.0 (25)		38.2 (30)	38.5 (35)	39.9 (20)	54.9 (25)	
		branches	27.5 (30)	27.2 (25)	30.6 (20)	31.5 (35)		19.2 (25)	33.8 (35)	34.9 (30)	44.0 (20)	
		Total Root	8.8 (25)	10.5 (20)	14.7 (35)	14.9 (30)		16.0 (20)	25.9 (25)	26.8 (30)	27.7 (35)	
		residual root	8.5 (25)	10.3 (20)	14.7 (35)	14.8 (30)		15.9 (20)	25.7 (25)	26.4 (30)	27.4 (35)	
		new root	0.0* (35)	0.1 (30)	0.1 (20)	0.3 (25)		0.2 (20)	0.2 (25)	0.2 (35)	0.4 (30)	
12	30/20	Total Shoot	84.0 (25)	87.7 (30)	87.9 (20)	88.0 (A)	88.3 (15)	65.9 (25)	69.0 (15)	71.0 (A)	72.5 (20)	74.5 (30)
		stem	38.5 (15)	40.9 (25)	45.1 (A)	52.1 (30)	57.0 (20)	30.8 (30)	42.5 (25)	51.3 (A)	52.3 (15)	54.4 (20)
		branches	30.9 (20)	35.6 (30)	43.1 (25)	42.9 (A)	49.8 (15)	16.7 (15)	18.1 (20)	19.7 (A)	23.4 (25)	43.7 (30)
		Total Root	11.4 (15)	11.7 (A)	12.1 (20)	12.3 (30)	16.0 (25)	25.6 (30)	27.5 (20)	28.3 (A)	31.0 (15)	34.1 (25)
		residual root	10.7 (20)	11.4 (15)	11.7 (A)	12.1 (30)	15.3 (25)	24.8 (30)	25.9 (20)	26.2 (15)	28.3 (A)	33.4 (25)
		new root	0.0 (A)	0.0 (15)	0.2 (30)	0.7 (25)	1.4 (20)	0.0 (A)	0.7 (25)	0.8 (30)	1.6 (20)	4.8 (15)

1 Mean of 3 replicates

2 Mean of 2 replicates

* Samples too small to be assessed.

Note: Horizontal lines join treatment means that are not significantly different at the $P_{0.05}$ significance level according to Duncan's multiple range test (Experiment 4, 6, 9, 10, 12) or Student's t-test (Experiment 5,7).

APPENDIX VII(A)

Stem and branch needle desiccation of root-pruned seedlings three weeks after replanting under various air and soil temperatures. Bracketed values indicate soil temperatures in °C. 'A' represents soil temperature the same as air temperature .

Experiment Number	Day/Night Air Temperature (°C)	Needle Desiccation (%)[1]	
		Stem Needles	Branch Needles
4	15/5	19.53 (A) 27.50 (15) 27.81 (10)	20.21 (A) 22.38 (15) 32.50 (10)
5	15/5	22.41 (5) 23.29 (20)	13.33 (5) 14.20 (20)
6	20/10	35.79 (15) 51.93 (A) 65.00 (10)	15.02 (15) 48.12 (A) 60.10 (10)
7	20/10	45.10 (25) 51.82 (20)	35.92 (25) 46.10 (20)
9	25/15	46.82 (A) 47.34 (2) 50.24 (25) 63.26 (15) 70.28 (10)	46.70 (25) 46.75 (20) 49.80 (15) 50.72 (A) 59.88 (10)
10	25/15	38.55 (30) 41.08 (20) 41.44 (25) 51.75 (35)	21.12 (25) 24.32 (30) 39.84 (20) 44.60 (35)
12	30/20	26.83 (A) 29.44 (25) 41.24 (30) 50.99 (20) 57.26 (15)	27.22 (25) 30.32 (A) 37.42 (30) 40.77 (20) 56.07 (15)
13	30/20	34.90 (30) 36.68 (25) 47.18 (35) 59.62 (40)	36.16 (30) 39.90 (25) 40.0 (35) 61.70 (40)

1 Values are means of 2 replicates.

Note: Horizontal lines join treatment means that are not significantly different at $P_{0.05}$ significance level according to Duncan's multiple range test or Student's t-test.

APPENDIX VII(B)

Changes in the relative water content of needles of root-pruned and intact seedlings at various soil and air temperatures. Bracketed values indicate initial measurement (0), measurement after one week (1) and measurement after three weeks (3).

Day/Night Air Temperature (°C)	Soil Temperature (°C)	Daily Heat Sum of Soil (degree-hours)	Relative Water Content of Needles (%)[1]	
			Root-Pruned	Intact
15/5	5	120	82.7 87.5 90.6 (3) (1) (0)	85.5 88.0 90.6 (3) (1) (0)
	10	240	85.9 86.0 86.4 (0) (3) (1)	85.7 85.9 86.6 (1) (0) (3)
	15/5	280	82.6 84.7 85.9 (3) (1) (0)	85.9 87.6 90.7 (0) (1) (3)
	15	360	85.8 85.9 88.7 (3) (0) (1)	85.9 90.5 91.5 (0) (1) (3)
	20	480	85.3 89.2 90.6 (3) (1) (0)	90.0 90.6 91.7 (3) (0) (1)
20/10	10	240	71.2 73.2 86.6 (3) (1) (0)	82.8 86.6 87.2 (1) (0) (3)
	15	360	76.0 77.9 86.6 (1) (3) (0)	86.6 86.6 91.1 (1) (0) (3)
	20/10	400	78.6 85.5 86.6 (3) (1) (0)	86.6 87.6 90.6 (0) (3) (1)
	20	480	85.2 86.7 86.9 (1) (3) (0)	86.9 87.0 87.7 (0) (1) (3)
	20	480	74.8 76.9 89.3 (3) (1) (0)	85.9 86.3 89.3 (3) (1) (0)
	25	600	85.1 85.1 86.9 (3) (1) (0)	86.9 88.7 89.6 (0) (1) (3)
	25	600	71.6 82.8 89.3 (3) (1) (0)	84.0 86.0 89.3 (1) (3) (0)
25/15	10	240	70.8 76.8 89.9 (3) (1) (0)	83.2 85.3 89.9 (3) (1) (0)
	15	360	64.6 74.3 89.9 (3) (1) (0)	84.9 86.8 89.9 (3) (1) (0)
	20	480	76.3 80.5 89.9 (1) (3) (0)	84.1 87.7 89.9 (3) (1) (0)
	20	480	74.5 83.2 88.0 (1) (3) (0)	86.0 88.0 89.4 (1) (0) (3)

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APPENDIX VII(B) (Cont'd)

Day/Night Air Temperature (°C)	Soil Temperature (°C)	Daily Heat Sum of Soil (degree-hours)	Relative Water Content of Needles (%)[1]					
			Root-Pruned			Intact		
25/15	20	480	76.0 (1)	76.8 (3)	86.0 (0)	85.0 (1)	85.9 (0)	87.3 (3)
	25/15	520	78.8 (3)	82.8 (1)	89.9 (0)	84.2 (3)	87.1 (1)	89.9 (0)
	25/15	520	74.9 (3)	74.9 (1)	85.9 (0)	85.9 (0)	86.2 (1)	86.6 (3)
	25	600	80.0 (1)	81.4 (3)	89.9 (0)	84.0 (3)	88.0 (1)	89.9 (0)
	25	600	78.1 (3)	81.2 (1)	88.0 (0)	88.0 (0)	88.2 (1)	89.8 (3)
	25	600	69.2 (1)	77.9 (3)	85.9 (0)	85.9 (0)	86.8 (1)	87.6 (3)
	30	720	79.9 (3)	80.5 (1)	88.0 (0)	86.7 (3)	87.7 (1)	88.0 (0)
	35	840	79.9 (1)	81.2 (3)	88.0 (0)	86.6 (1)	87.2 (3)	88.0 (0)
30/20	15	360	65.7 (3)	69.9 (1)	88.7 (0)	83.2 (3)	83.3 (1)	88.7 (0)
	20	480	70.3 (3)	70.7 (1)	88.7 (0)	83.9 (3)	84.2 (1)	88.7 (0)
	25	600	75.2 (3)	75.8 (1)	88.7 (0)	85.4 (3)	86.5 (1)	88.1 (0)
	25	600	74.6 (3)	79.1 (1)	86.9 (0)	80.2 (3)	82.5 (1)	86.9 (0)
	30/20	640	76.6 (1)	81.4 (3)	88.7 (0)	84.9 (3)	85.8 (1)	88.7 (0)
	30	720	73.4 (1)	75.7 (3)	88.7 (0)	85.6 (1)	86.4 (3)	88.7 (0)
	30	720	78.5 (3)	80.3 (1)	86.9 (0)	83.4 (3)	86.9 (0)	87.8 (1)
	35	840	79.5 (3)	82.9 (1)	86.9 (0)	84.4 (3)	86.9 (0)	87.4 (1)
	40	960	73.0 (3)	82.6 (1)	86.9 (0)	86.9 (0)	88.7 (1)	90.1 (3)

1 Mean value of 6 replicates.

Note: Horizontal lines join treatments that are not significantly different at the $P_{0.05}$ significance level according to Duncan's multiple range test or Student's t-test.